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A REVISION OF THE LAKE VICTORIA
HAPLOCHROMIS SPECIES
(PISCES, CICHLIDAE)
PART VII



P. H. GREENWOOD
AND
J. M. GEE

BULLETIN OF
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ZOOLOGY Vol. 18 No. 1
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A REVISION OF THE LAKE VICTORIA
HAPLOCHROMIS SPECIES
(PISCES, CICHLIDAE)

PART VII



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Pp. 1-65; 35 *Text-figures*

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A REVISION OF THE LAKE VICTORIA *HAPLOCHROMIS* SPECIES

By P. H. GREENWOOD & J. M. GEE

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INTRODUCTION

MOST of the species described in this paper were collected during experimental and exploratory trawling operations in the northern waters of Lake Victoria.

Trawling has revealed the existence of numerous undescribed, apparently benthic, species living in sublittoral habitats at depths down to more than 200 feet.

Ecological information on these fishes is still very scanty. Many of the species seem to have a wide depth range (for example from 30 to 100 feet, or for species found only at greater depths, from 70 to 200 feet), but few extend into the littoral and immediately sublittoral zones. Others seemingly have a more circumscribed depth range being confined to depths of from 50 to 100 feet.

This supposed restriction to offshore areas is inferred from the absence of "trawl species" in catches made by other fishing gear in the littoral and inshore sublittoral zones. Such reasoning has, of course, certain weaknesses. For instance, compared with a trawl, the nets used to sample the littoral and immediately sublittoral zones are highly size selective and thus might not catch small fishes. However, adult individuals of several "trawl species" are large enough to be caught by seine- and gillnets, yet none of these species has been caught, despite intensive collecting.

Conversely, only one predominantly littoral species, *Haplochromis obesus*, has been caught in deeper water. We have, however, certain reservations about the identity

of these specimens which could be representatives of a deep-water species closely related to *H. obesus* (see appendix, page 63).

The geographical distribution of "trawl species" within the lake is still unknown since all the available collections are from the northern (Uganda) part of Lake Victoria. Even within this area, however, there are indications from some species of interpopulational differences in certain morphological characters. Doubtless our descriptions of the new species will have to be modified when specimens from other areas become available. Nevertheless, we are moderately confident that such additional data will not alter the specific validity of the taxa described below.

We have assumed that most, if not all, of the known "trawl species" live on or near the bottom for at least part of the day: these assumptions are based especially on the nature of the food of those species whose diet is known, and on the other ingested material found in the gut. But, we cannot overrule the possibility of fishes being caught while the net is sinking to the bottom or being hauled to the surface.

The present paper by no means covers all the new species that have been caught in trawling operations. The other species will be described in subsequent papers, where it is also proposed to discuss in more detail the relationships of the "trawl species" to each other and to the inshore species complexes.

***Haplochromis megalops* sp. nov.**

(Text-fig. 1)

HOLOTYPE: an adult male 75.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.57.) from Windy Bay, Napoleon Gulf.

The trivial name refers to the large eye.

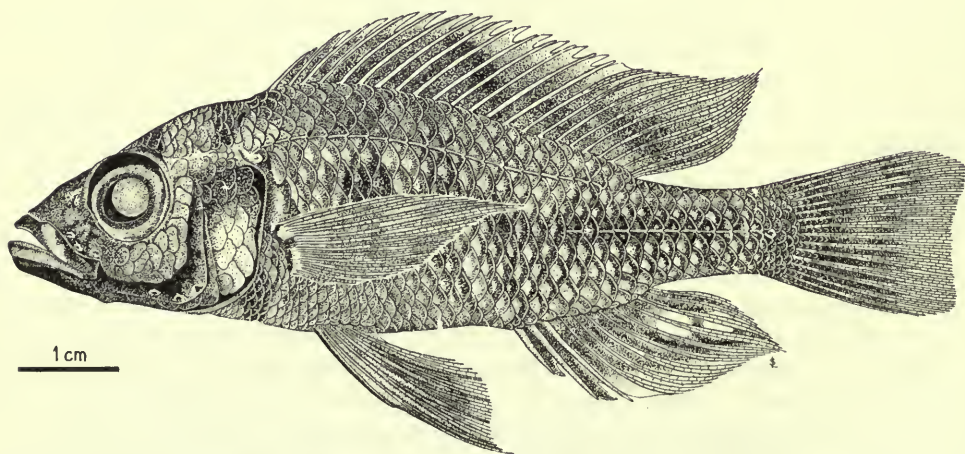


FIG. 1. *Haplochromis megalops*. Holotype. Drawn by Sharon Lesure.

DESCRIPTION: based on 27 specimens (including the holotype), 66.0–81.0 mm. S.L.

Depth of body 30.9–36.3 (mean, $M = 33.4$) % of standard length, length of head 32.0–35.6 ($M = 33.8$) %.

Dorsal head profile straight except for a slight curvature in the nuchal region, and sloping fairly steeply at 30°–40°.

Preorbital depth 11.1–15.4 ($M = 12.9$) % of head length, least interorbital width 22.7–28.0 ($M = 24.9$) %. Snout broader than long (1.1 [mode] to 1.3, rarely 1.4 times), its length 25.0–30.8 ($M = 27.5$) % of head; eye diameter 32.7–41.0 ($M = 36.4$), depth of cheek 17.3–22.6 ($M = 20.0$) %.

Caudal peduncle 15.3–19.2 ($M = 16.3$) % of standard length, 1.2 (rarely)–1.6 (mode 1.4) times as long as deep.

Mouth very slightly oblique; posterior tip of the maxilla reaching a vertical through the anterior part of the eye or, less commonly, to the anterior orbital margin. Jaws equal anteriorly or the lower jaw projecting very slightly, length of lower jaw 39.6–46.0 ($M = 43.3$) % of head, 1.8–2.3 (mode 2.0), rarely 1.7 or 2.4, times as long as broad.

Gill rakers: 10–12 (mode 11) on the lower part of the first gill-arch. The lower 2 or 3 rakers are reduced, and are followed by from 1 to 3 relatively slender rakers; the remainder are usually somewhat flattened, with the upper 1 or 2 often anvil-shaped.

Scales: ctenoid. Lateral line with 30 (f.3), 31 (f.6), 32 (f.12) or 33 (f.5) scales; cheek with 2 or 3 rows. Five to 6 (mode 5½) scales between the upper lateral line and the dorsal fin origin, 5–7 (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.3), 24 (f.17) or 25 (f.6) rays, comprising 14 (f.3), 15 (f.18) or 16 (f.5) spinous and 8 (f.4), 9 (f.17) or 10 (f.5) branched elements. Anal with 11 (f.8), 12 (f.16) or 13 (f.1) rays, comprising 3 spines and 8–10 branched rays. Pectoral 28.7–33.8 ($M = 30.5$) % of standard length. Pelvics with the first ray produced (apparently in both sexes, but only 1 female fish is available). Caudal truncate, scaled on its basal half.

Teeth. Except posteriorly in the upper jaw, the *outer* teeth in most specimens are either bicuspid, or an admixture of bi- and weakly bicuspid. The teeth are compressed, relatively stout, and slightly recurved. In some fishes most outer teeth are unicuspid and caniniform, while in other specimens unicuspid occur amongst the more numerous bicuspid; only rarely are all the outer teeth unicuspid. The outer teeth in both jaws of an individual may be similar in form, or there can be relatively more unicuspid present in the lower jaw.

The posterior outer teeth of the upper jaw are usually unicuspid and caniniform, and are often relatively large. In a few specimens, however, these teeth are similar to those occurring laterally in the jaw.

There are 48–60 ($M = 52$) teeth in the outer row of the upper jaw.

The *inner* teeth are generally tricuspid, but weakly so, and in a few fishes are unicuspid. All inner teeth are implanted somewhat obliquely, and are arranged in 2 rows (infrequently in 1 row) in the upper jaw, and in a single row in the lower jaw.

Osteology. The syncranium of *H. megalops* is typically that of a structurally generalized *Haplochromis* species, and as such does not depart from the type found in, for example, *H. macrops*, *H. nubilus*, *H. phytophagus* or *H. obliquidens*.

The *neurocranium* has a decurved preorbital profile and has the proportions of a generalized skull type. The openings to the cephalic lateral line canals are, however, somewhat larger than those of the species mentioned above. In contrast, the lateral line system in the dentary of *H. megalops* is not noticeably enlarged.

The lower pharyngeal bone is fine, its dentigerous surface slightly broader than long (1.1–1.2 times). The teeth are slender and cuspidate, and are arranged in 30–36 rows. In most specimens the teeth of the median rows are a little coarser than the others.

Coloration. The colours of live males are unknown; females are silvery (darker on the dorsal surfaces), with the dorsal fin hyaline, and the pelvic and anal fins pale yellow.

Preserved material: Males (adult and sexually active) brownish grey above the mid-lateral line, dusky silver below (the amount of silver visible is variable, with in extreme cases most of the ventral body half solid black save for a fine silvery sheen on the lateral aspects of the belly). A few fishes show traces of about 4 dark blotches arranged along the midlateral line of the flanks.

The snout is almost entirely black, as is the preorbital region, the lower jaw and the ventral aspects of the preoperculum; in some specimens the posterior opercular margin (otherwise silver) has a broad black margin. Two intensely black bars cross the snout, but these are only faintly discernible on the general dusky coloration of this region. A medially interrupted occipital band originates near the dorso-posterior margin of the orbit, and the nuchal region is crossed by a dark band (of variable distinctness) which originates near the opercular-preopercular junction.

Dorsal fin dusky, as are the caudal and anal fins, the latter being of variable intensity, almost black in some specimens. The anal ocelli are small, and dead white. The pelvic fins are black.

The single female available is extensively stained by rust from the metal container in which it was preserved. Thus, nothing can be said about its preserved coloration.

Ecology. Habitat. At present, the species is known from only 2 localities, one a small bay in the Napoleon Gulf near Jinja, the other in Pilkington Bay. In both places the habitat is sheltered, the water from 10–30 feet deep, and the substrate of mud or of interposed mud and sand patches.

Food. Seven of the 25 guts examined were empty. In the remainder, the predominant ingested material is macerated dipterous (?chironomid) larvae, together with small quantities of bottom mud. Chironomid pupae are also present in 8 stomachs.

Breeding. The single female examined (74 mm. S.L.) is in an advanced stage of oogenesis; both ovaries are equally developed. All the males (66–81 mm. S.L.) are adult.

Diagnosis and affinities. *Haplochromis megalops* closely resembles another new species, *H. piceatus* (see p. 7); preserved specimens of the 2 species are readily confused on superficial examination. However, *H. megalops* has a larger eye (32.7–41.0, mean 36.4% of head, cf. 29.0–34.0, mean 32.3% in *H. piceatus*), and a much

shallower preorbital (11.1–15.4, mean 12.9% of head, cf. 13.6–17.8, mean 15.3%). There are other, but less trenchant differences, including dental characters (cf. p. 5 and p. 8).

Superficially, *H. megalops* resembles *H. cinereus*, but is distinguished from that species by its more numerous gill rakers (10–12, mode 11, cf. 7–9, mode 7), shallower preorbital (11.1–15.4, mean 12.9% head, cf. 15.0–18.0, mean 16.4%), larger eye (32.7–41.0, mean 36.4% head, cf. 26.2–32.0, mean 28.7%), longer lower jaw (39.6–46.0, mean 43.3% head, cf. 34.6–41.3, mean 37.7%) and by differences in the oral and pharyngeal dentition (see Greenwood, 1960, p. 240).

From *H. macrops*, another large-eyed species of the generalized *Haplochromis* species group (or groups), *H. megalops* is distinguished by its higher gill raker count (10–12, mode 11, cf. 8–11, mode 9) and its longer lower jaw (39.6–46.0, mean 43.3% head, cf. 38.0–42.5, mean 39.5%); the coloration of preserved specimens also differs (see Greenwood *op. cit.*, p. 236).

Haplochromis megalops is structurally and trophically a generalized species, and thus it is difficult to suggest its phyletic affinities in any more precise terms. Apart from *H. piceatus*, the species which it most closely resembles are *H. macrops*, and *H. cinereus* (see Greenwood, 1960, pp. 236–239, and 239–242).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality				Collector
	UGANDA				
B.M. (N.H.) 1968.8.30.57 (Holotype)	Windy Bay, Napoleon Gulf	.	.	.	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.58–73	Windy Bay	.	.	.	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.74–88	Pilkington Bay	.	.	.	E.A.F.F.R.O.

Haplochromis piceatus sp. nov.

(Text-figs 2–4)

HOLOTYPE: an adult male 88.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.39) from the Napoleon Gulf opposite Jinja Prison.

Named with reference to the coloration of preserved specimens (from the Latin, meaning smeared with pitch).

DESCRIPTION: based on 16 specimens (including the holotype) 67–90 mm. S.L.

Depth of body 32.0–35.3 ($M = 33.3$) % of standard length, length of head 32.8–35.5 ($M = 34.1$) %.

Dorsal head profile straight, except for slight curvature in the nuchal region, sloping at an angle of 35°–40°.

Preorbital depth 13.6–17.8 ($M = 15.3$) % of head, least interorbital width 21.8–25.0 ($M = 23.6$) %. Snout as long as broad or very slightly broader than long (1.1 times), its length 27.2–32.2 ($M = 28.3$) % of head; eye diameter 29.0–34.0 ($M = 32.3$), cheek depth 16.7–21.0 ($M = 18.9$) %.

Caudal peduncle 17.3–20.9 ($M = 19.1$) % of standard length, 1.6–2.0 (modal range 1.6–1.8) times as long as deep.

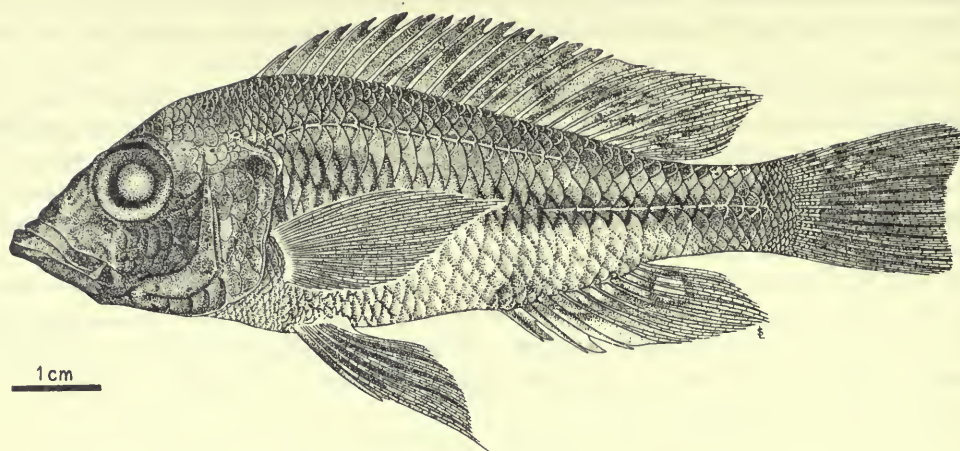


FIG. 2. *Haplochromis piceatus*. Holotype. Drawn by Sharon Lesure.

Mouth slightly oblique, the jaws equal anteriorly or, more commonly, the lower projecting slightly; length of lower jaw 41.8–45.0 ($M = 43.5$) % of head, 2.0 (mode)–2.6 times its breadth (in one exceptional specimen 2.8 times). Posterior tip of the maxilla reaching a vertical through the anterior part of the eye or only as far as the anterior orbital margin.

Gill rakers: 12 (mode) or 13, rarely 11 or 15, on the lower part of the first gill arch. The lower 2–5 rakers reduced, the remainder of varied form (even in one individual), usually short, or slender, or flattened and with the uppermost raker anvil-shaped in outline; some lower rakers may also be anvil-shaped or lobed.

Scales: ctenoid. Lateral line with 32 (f.7), 33 (f.7) or 34 (f.2) scales, cheek with 2 or 3 rows. Five to 6 scales between the dorsal fin origin and the upper lateral line, 5–6 (mode) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.11) or 25 (f.4) rays, comprising 14 (f.2) or 15 (f.14) spinous and 9 (f.10) or 10 (f.6) branched elements. Anal with 11 (f.11) or 12 (f.5) rays, comprising 3 spines and 8 or 9 branched rays. Pectoral 27.0–32.3 ($M = 29.6$) % of standard length. Pelvics with the first ray produced in both sexes, but proportionately longer in males. Caudal truncate, scaled on its proximal half.

Teeth. The *outer teeth* (Text-fig. 3) situated posteriorly in the upper jaw of most specimens are unicuspid or tricuspid, those placed posterolaterally are tricuspid; in a few specimens these teeth are not, however, differentiated from the other outer teeth. The posterior teeth are deeply embedded in the gum tissue and are difficult to expose (*cf.* the situation in *H. megalops* where these teeth are unicuspid and readily exposed).

The anterolateral and anterior teeth in the upper jaw, and all outer teeth in the lower jaw, are slender, compressed and unequally bicuspid, with the major cusp produced and slender, and the minor cusp short but clearly demarcated.

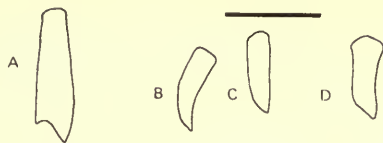


FIG. 3. *Haplochromis piceatus*. Jaw teeth. A, C and D in anterior view, B in lateral view. A: an anterior upper jaw tooth from a small individual (67 mm. S.L.); C and D: posterior upper teeth from a larger fish (85 mm. S.L.). Scale equals 0.5 mm. for A, 1 mm. for B-D.

There are 54-74 ($M = 64$) outer teeth in the upper jaw. The *inner* teeth are tricuspid and generally implanted somewhat obliquely; there are 2 (rarely 3) series in the upper jaw, and 1 or 2 in the lower.

Osteology. The syncranium of *H. piceatus* is indistinguishable from that of *H. megalops* (see p. 6); that is, it is of the generalized type.

The *lower pharyngeal bone* (Text-fig. 4) is fine, with its dentigerous surface slightly broader than long, and carries 36-40 rows of slender, cuspidate teeth.

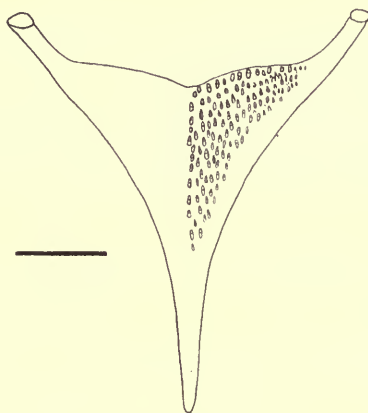


FIG. 4. *Haplochromis piceatus*. Lower pharyngeal bone; teeth indicated on left side. Scale equals 2 mm.

Coloration. The colours of live fishes are unknown. *Preserved material.* *Males* (adult and sexually active), are almost indistinguishable from males of *H. megalops* but differ slightly in that the demarcation between the lighter upper surfaces and the darker flanks is less obvious, the general coloration being greyer. Also, in *H. piceatus* there are no signs of any midlateral dark blotches.

Females are an almost uniform silvery-yellow, but darker dorsally; there is a very faint indication of a narrow midlateral stripe on the posterior third of the body, terminating at the base of the caudal fin. The dorsal and caudal fins are greyish, the latter weakly maculate on its upper half, and somewhat darker near the base. The anal and pelvic fins are hyaline.

Ecology. Habitat. The material on which this description is based came from a trawl haul in water 45–60 feet deep, over a mud bottom, in the relatively sheltered Napoleon Gulf.

Food. Four of the 14 guts examined were empty, and the remainder contained very little ingested material. Bottom mud and dipterous pupae (probably Chironomidae) were identified.

Breeding. All 16 specimens (67–90 mm. S.L.) are adult. One female has a few larvae in the buccal cavity, thus suggesting that the species is a mouth brooder. Three of the 4 females known have the right ovary, noticeably larger than the left; in the fourth individual (probably at an early stage of oogenesis) the ovaries are of almost equal size.

Diagnosis and affinities. *Haplochromis piceatus* is very similar to *H. megalops*; characters distinguishing the 2 species are given on p. 6. The principal dental differences lie in the presence of some tricuspid teeth posterolaterally in the upper jaw of most *H. piceatus* individuals, and in the absence of caniniform unicuspid anteriorly and anterolaterally in the outer tooth row of all individuals. The tendency for the posterior upper teeth of *H. piceatus* to be deeply embedded is another difference between the species.

Haplochromis piceatus also resembles *H. cinereus* and *H. macrops* (see Greenwood, 1960, pp. 236–239, and 239–242); it is distinguished from both species principally by its higher gill raker count and longer lower jaw. In other morphometric characters, however, *H. piceatus* approaches these species more closely than does *H. megalops*.

Remarks on the phyletic position of *H. megalops* (see p. 7) apply equally to *H. piceatus*.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.39 (Holotype)	Napoleon Gulf, nr. Jinja prison .	. E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.40–56	Napoleon Gulf, nr. Jinja prison .	. E.A.F.F.R.O.

Haplochromis paropius sp. nov.

(Text-figs 5–7)

HOLOTYPE: an adult male 69.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.89) from near Bulago island.

The trivial name (from the Greek for “eye shade”) refers to the prominent lachrymal stripe.

DESCRIPTION: based on 34 specimens (including the holotype) 63.0–87.0 mm. S.L.

Depth of body 35.0–40.3 ($M = 37.4$) % of standard length, length of head 31.5–35.8 ($M = 34.0$) %.

Dorsal head profile gently curved (rarely straight), sloping steeply at 40°–45°.

Preorbital depth 13.6–17.4 ($M = 15.6$) % of head, least interorbital width 18.3–28.0 ($M = 23.1$) %. Snout 1.1–1.5 (mode 1.2) times as broad as long, its length

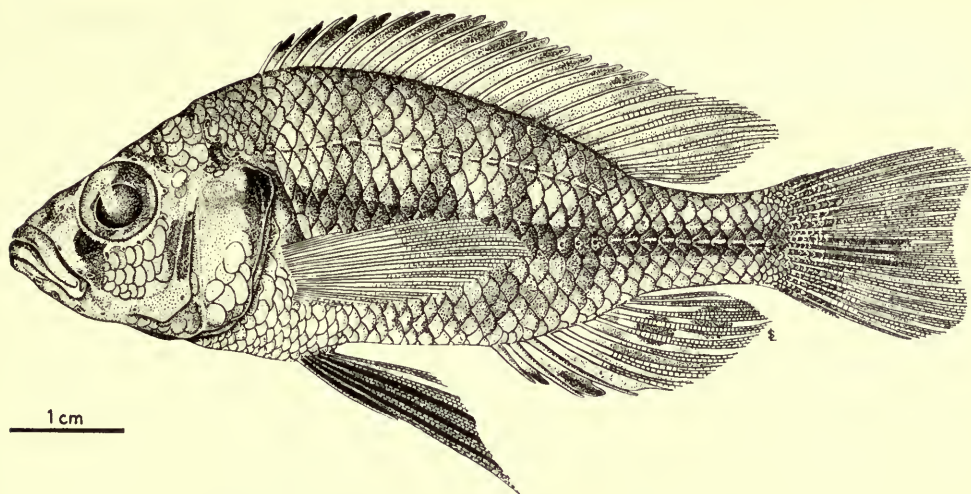


FIG. 5. *Haplochromis paropijs*. Holotype. Drawn by Sharon Lesure.

25.0–31.9 ($M = 29.1$) % of head; eye diameter 28.0–34.8 ($M = 31.9$), depth of cheek 18.1–24.2 ($M = 21.3$) %.

Caudal peduncle 15.6–20.6 ($M = 18.8$) % of standard length, 1.3 (rare) to 1.9 (mode 1.6) times as long as deep.

Mouth horizontal (the usual condition) to slightly oblique (*ca* 15°); jaws equal anteriorly. Lower jaw 39.5–45.5 ($M = 41.2$) % of head, 1.5–1.9 (modal range 1.5–1.6) times as long as broad; a weak mental protuberance is visible in many specimens.

Posterior tip of the maxilla reaching a vertical through the anterior part of the eye or somewhat posterior to that point (rarely only reaching a vertical through the anterior orbital margin).

Gill rakers: 8–10 (mode 9), the lower 1–3 rakers reduced, the upper 2–4 flattened and club-like, branched or anvil-shaped; other rakers of various shapes, from short and stout to relatively slender.

Scales: ctenoid; lateral line with 30 (f.1), 31 (f.13), 32 (f.13) or 33 (f.3), cheek with 3 (rarely 4) rows. Five to 7 (mode 6) scales between the upper lateral line and the dorsal fin origin, 5–7 (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.8), 24 (f.23) or 25 (f.2) rays, comprising 15 (f.27) or 16 (f.6) spinous and 8 (f.12) or 9 (f.21) branched elements. Anal with 11 (f.23) or 12 (f.9) rays, comprising 3 spines and 8 or 9 rays. Pectoral fin 27.9–34.7 ($M = 31.7$) % of standard length. Caudal truncate scaled on its proximal half. Pelvics with the first ray produced in both sexes, but relatively longer in adult males.

Teeth. Except posteriorly, the *outer* teeth in *both* jaws are relatively stout and bicuspid (Text-fig. 6A), with compressed and slightly expanded crowns. Posteriorly and posterolaterally in the upper jaw there are, usually, 2 to 5 enlarged and near caniniform unicuspid teeth, preceded by a variable number of compressed tricuspid.

In some fishes only the tricuspid are present and in a few others the posterior teeth are identical with those situated anteriorly and laterally.

There are 56-74 ($M = 62$) outer teeth in the upper jaw.

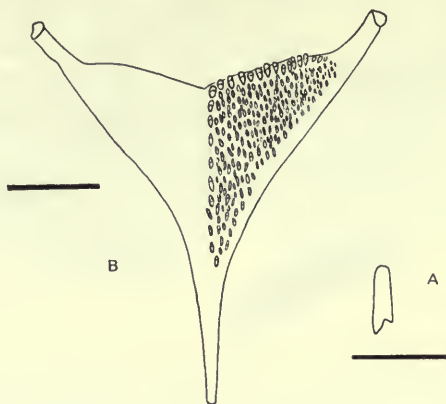


FIG. 6. *Haplochromis parapius*. A: Upper jaw tooth (anterior view). B: Lower pharyngeal bone. Scale equals 1 mm. for A, 2 mm. for B.

Inner teeth are tricuspid, compressed, and arranged in 2 or 3 (rarely 4) rows in the upper jaw and 2 (less frequently 1 or 3) rows in the lower.

Osteology. The neurocranium of *H. parapius* is typically that of the generalized *Haplochromis* type (as seen, for example, in such species as *H. nubilus*, *H. macrops* and *H. brownae*, etc.) with a gently curved preorbital dorsal profile, and relatively

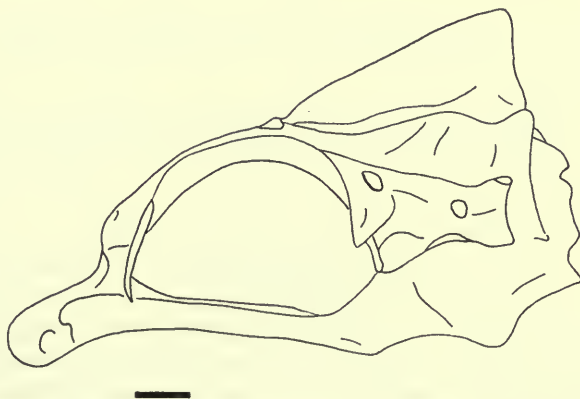


FIG. 7. *Haplochromis parapius*. Neurocranium; left lateral view. Scale equals 2 mm.

broad in the otic and interorbital regions (Text-fig. 7). The lateral line tubes and pores are not noticeably hypertrophied.

The *dentary* and *premaxilla* are also of the generalized type, although the dentary is more elongate and has slightly enlarged lateral line tubes. The lateral line tubules on the *preorbital* are also somewhat hypertrophied.

The *lower pharyngeal bone* is fine, its triangular dentigerous surface slightly broader (1.1-1.2 times) than long (Text-fig. 6B). The teeth are slender, cuspidate and fairly densely arranged in 38-46 rows, the total impression being that of a dental "felt". In some specimens, teeth in the median rows are slightly coarser than the lateral teeth.

Coloration in life. Adult, sexually active males: ground colour of body greenish, as are the snout and lips (the lower sometimes blueish); the belly is silvery. Dorsal surface of the head and body, anterior part of the belly, the opercular region and the branchiostegal membrane red (deepest red dorsally and often on the anterior ventral surfaces, otherwise orange-red). There is a pronounced, dark lachrymal stripe, a fainter transverse bar across the snout and often traces of 3 or 4 faint vertical bars on the flanks; in many individuals a faint dark midlateral longitudinal band is visible.

Dorsal fin dark green proximally, the distal part either with an overall red flush or the red pigment aggregated into spots and streaks on the soft part of the fin. Caudal green proximally, hyaline or flushed with red distally. Anal fin hyaline to white, sometimes with a dusky base; ocelli yolk-yellow. Pectoral fins in some individuals greenish, otherwise hyaline. Pelvics black.

Quiescent males are generally similar in coloration to active fishes, but the red body and head colours are much fainter, and the pelvics are dusky.

Females are dark grey (with faintly greenish undertones) dorsally, shading to silver on the flanks and belly below a distinct but interrupted dark midlateral stripe. The dorsal fin often has a red flush over the soft part, but the spinous part is hyaline. The anal fin in yellow; all other fins are hyaline.

Preserved material. Males: ground colour light brown, shading to silvery-white on the chest and belly; the flank scales in sexually active fishes have broad, dark margins. In most fishes a wide, dark midlateral band runs from the posterior opercular margin to the caudal origin; this band is sometimes broken, and it may even be entirely absent. When absent it is replaced by 5 fairly distinct vertical bars on the flanks; each bar tapers dorsally and ventrally, and none reaches the body outline. Faint to fairly distinct indications of these bars are sometimes discernible in fishes with a well-developed midlateral band.

A distinct, vertical lachrymal band runs from the orbit to immediately behind the posterior tip of the maxilla; it is always visible although of very variable intensity. In some specimens another short vertical bar is present along the vertical limb of the preoperculum. Two parallel transverse bars cross the snout, and a third, medially interrupted and broader bar crosses the occiput from orbit to orbit. This band may appear as a dorsal continuation of the lachrymal stripe.

Dorsal fin hyaline, with dusky lappets, sometimes with dark blotches between the soft rays and at the bases of the spines. Caudal hyaline, but with some darkening of the membrane between the central rays. Anal hyaline to greyish, the ocelli usually greyish-white but sometimes dead-white. Pelvic fins black.

Females have a preserved coloration very like that of males (including dark dorsal lappets and a dark base to the dorsal fin), but the ventral surfaces of the body are silvery white, the flank scales are without dark margins, and the cephalic markings are much less intense (or even absent).

Ecology. Habitat. *Haplochromis paropius* has been caught in several areas of northern Lake Victoria, but always over a mud substrate, in water 50–100 feet deep, and in off-shore regions.

Food. The intestine is long and coiled, the stomach large and distensible, thus suggesting a vegetarian diet. The contents of 20 guts were examined, and seem to confirm this supposition. All contain large quantities of blue-green algae and diatoms, and smaller amounts of other plant material. Eight of these guts contain, in addition, fragmentary remains of larval Diptera (probably chironomids).

Of the plant material, only the diatoms show any appreciable signs of digestion; the blue-green algae are apparently undigested.

Breeding. All the specimens examined (63–87 mm. S.L.) are adult.

Diagnosis and affinities. Structurally, *H. paropius* is a generalized species in all respects except for the long gut which is a specialization associated with essentially vegetarian feeding habits.

The coloration of adult males seems to distinguish *H. paropius* from most of the other generalized *Haplochromis* species described so far (and including those with vegetarian diets). Exceptions to this statement are *H. erythrocephalus* and *H. cinctus*, both new species described in this paper (see pp. 19 and 15 respectively).

Haplochromis erythrocephalus is distinguished by several characters (including details of coloration) and *H. cinctus* principally by colour differences; *H. paropius* is compared with these species on pp. 23 and 18. The resemblance between *H. cinctus* and *H. paropius* is very close indeed, but because the differences involve male coloration we attach great importance to them, especially since the species are sympatric. On anatomical grounds, *H. cinctus* and *H. paropius* would seem to qualify as sibling species.

Superficially, *H. paropius* resembles *H. lacrimosus* (see Greenwood, 1960). Unfortunately the live coloration of adult male *H. lacrimosus* is unknown, but there are certain similarities in the preserved coloration of the two species. However, there are also several differences (*cf.* p. 13 above with p. 231 in Greenwood *op. cit.*) and it seems likely that the differences in live colours may be fairly marked. The principal anatomical characters distinguishing the species are the longer lower jaw of *H. paropius* (39.5–45.5, $M = 41.2\%$ head, *cf.* 31.4–41.3, $M = 37.1\%$ in *H. lacrimosus*), the long, coiled gut, and the larger number of outer teeth in the upper jaw (56–74, $M = 62$, *cf.* 40–60, $M = 50$ for *H. lacrimosus*).

Another species bearing a superficial resemblance to *H. paropius* is *H. melanopus* Regan, 1922. This species is very poorly known and has not yet been revised. It is represented only by the 3 syntypes on which Regan based his description (Regan, *op. cit.*, fig. 1). *Haplochromis melanopus* differs from *H. paropius* in having more gill rakers on the lower part of the first arch (11 or 12, *cf.* 8–10, mode 9) and a much shorter lower jaw (31.0–32.6% of head, *cf.* 39.5–45.5, $M = 41.2\%$). Until more is known about *H. melanopus* the comparison cannot be carried further.

From other generalized species with an essentially bicuspid outer dentition, *H. paropius* is distinguished by its coloration, its longer gut, and by various combinations of morphometric characters. For accounts of those species see Greenwood, 1960, and pp. 4–10 of this paper.

Certain other deeper water species resemble *H. paropius* anatomically and in some cases, in their coloration as well (for example, *H. cinctus*, see p. 17). We are studying 3 such species at present but cannot yet describe them in full detail. However, from the information we have it is clear that *H. paropius* is distinct.

Haplochromis paropius is derived from the same stem as the other anatomically generalized *Haplochromis* species in Lake Victoria; for the moment it is not possible to suggest any more precise relationships. Despite similarities in male coloration it seems unlikely that *H. paropius* is closely related to *H. erythrocephalus*, which apparently belongs to a different lineage within the complex of generalized species (see p. 23).

Notes on three specimens from near Mwama island

Three fishes (64.0, 65.5 and 69.0 mm. S.L.; all adult and sexually active males) appear to be very atypical members of this species. The specimens came from a single trawl haul made at depths ranging from 70–200 feet, over both hard (rock and sand) and soft mud substrates. The trawl was shot in a bay on the south side of Mwama island and hauled at a place some distance off-shore in the open lake.

In general facies the 3 fishes closely resemble other specimens of *H. paropius*, but in 2 specimens the eye is larger (36.4 and 39.1% of head) and in the third the eye diameter is in the upper range known for *H. paropius* (34.8%). All 3 specimens also differ somewhat in coloration, viz., the dorsal head colour is lighter red (i.e. more orange than red) and there is no trace of red pigment on the anterior chest region or on the belly (these regions being white). Finally, the branchiostegal membrane is white and not black as in other *H. paropius* males.

With only 3 specimens available we cannot evaluate the significance of these differences. But, judging from our knowledge of other species related to *H. paropius* (including several as yet undescribed species) the 3 Mwama fishes could well represent yet another species in the "*paropius*" complex.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.89 (Holotype)	Near Bulago isl. (80–90 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.90–117	S.W. and N.E. of Bulago isl. (55–75 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.118–123	Near Bulago isl. (80–90 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.124–126	Near Mwama isl. (70–200 feet)	E.A.F.F.R.O.

Haplochromis cinctus sp. nov.

(Text-fig. 8)

HOLOTYPE: an adult male 84.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.13) from a trawl haul made in water 70–200 feet deep, near Mwama island.

The trivial name (from the Latin for "girded") refers to the characteristic banding seen in males.

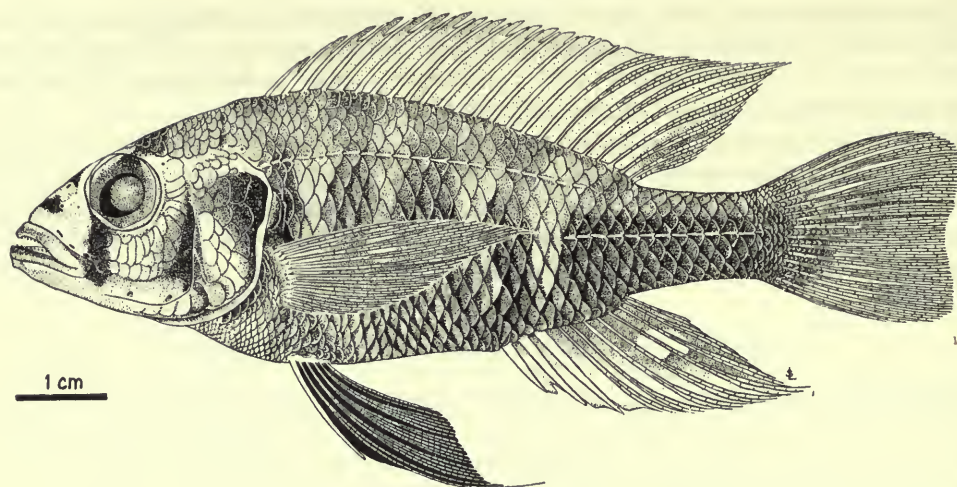


FIG. 8. *Haplochromis cinctus*. Holotype. Drawn by Sharon Lesure.

DESCRIPTION: based on 6 specimens 76.0–87.5 mm. S.L. The principal morphometric ratios are given below:

S.L.	D.†	H.†	Po. %	Io. %	Snt. %	Eye %	Ck. %	Lj %	C.P.†
76.0	36.9	33.3	15.8	25.7	30.4	31.6	19.8	39.5	18.4
81.0	38.2	33.4	14.8	25.9	29.1	33.3	21.5	40.8	17.9
84.0	36.9	32.7	16.4	27.2	31.0	34.6	20.0	43.5	15.5
84.0	37.0	32.2	18.5	25.2	33.3	36.3	21.5	41.8	19.0
86.5	38.1	34.7	16.0	24.3	30.0	30.0	20.0	40.0	16.8
87.8	36.6	35.4	16.1	25.2	29.0	30.6	21.5	41.8	19.0

† = % of standard length
% = % of head length

Dorsal head profile slightly curved, sloping at an angle of 40° – 50° ; in 2 specimens the snout profile slopes even more steeply than the head profile. Snout 1.1 (mode)–1.2 times broader than long.

Lower jaw horizontal or very slightly oblique, 1.5–1.8 times as long as broad. Jaws equal anteriorly. Posterior tip of the maxilla reaching a vertical through the anterior part of the eye or almost to the pupil.

Caudal peduncle 1.3–1.8 times as long as deep.

Gill rakers: 9 on the lower part of the first gill arch, the lower 1 or 2 rakers reduced, the upper 3–5 flattened, sometimes divided and anvil-shaped; intervening rakers of varied form, from relatively slender to relatively stout.

Scales: ctenoid; lateral line with 32 (f.5) or 33 (f.1) scales, cheek with 3 rows. Six and a half to 8 (mode $6\frac{1}{2}$) scales between the upper lateral line and the dorsal fin origin, 6–8 (mode 7) between the pectoral and pelvic fin bases. Scales on the ventral chest region noticeably smaller than those situated laterally on the chest, or those on the belly.

Fins. Dorsal with 23 (f.1) or 24 (f.5) rays, comprising 15 (f.4) or 16 (f.2) spines and 8 (f.3) or 9 (f.3) branched rays. Anal with 11 (f.2) or 12 (f.4) rays, comprising 3 spines and 8 or 9 branched rays. Pectoral 31.0–33.1 % of standard length. Pelvics with the first and second rays produced and filamentous. Caudal slightly emarginate, scaled on its proximal half.

Teeth. The *outer* teeth in the *upper jaw* are an admixture of stout, unequally bicuspid and tricuspid teeth, with the bicuspid predominating. Posteriorly, the teeth are unicuspid and caniniform. There are 50–64 teeth.

In the *lower jaw*, the *outer* teeth are stout and unequally bicuspid anteriorly and laterally, but tricuspid posteriorly and posterolaterally.

The *inner* teeth in both jaws are tricuspid, and are arranged in 2 rows.

Osteology. No complete skeleton is available. The *lower pharyngeal bone* has a triangular dentigerous surface, 1.2 times as broad as long. The teeth are bicuspid, relatively coarse, and are arranged in 30–38 rows, those of the 2 median rows being somewhat coarser than the lateral teeth.

Coloration in life. *Males:* dorsal surface of head and body light grey with a distinct orange overtone; light orange on the operculum and flanks, belly dark blue-black. The flanks are crossed by 3–5 dark vertical bars which extend from the belly to the upper lateral line; these bars have turquoise highlights, as do the lateral surfaces of the caudal peduncle. The lower jaw is grey, with a turquoise sheen; the branchiostegal membrane is sooty. The ventral limb of the preoperculum has a broad, dark blotch, and 2 distinct parallel dark bands cross the snout. Above each eye there is a dark spot, the spots from each side almost meeting in the midline.

The dorsal fin is hyaline, with orange-red lappets and similarly coloured (but fainter) streaks between the spines; very distinct orange-red spots occur between the branched rays. Caudal fin is hyaline but with a reddish-orange flush. Anal with a narrow greyish area at its base but becoming faintly reddish-orange distally; the ocelli are yolk-yellow.

The coloration of *live females* is unknown.

Preserved material. *Males:* Dorsal surface of the head and the upper part of the body light brown. Chest, belly and almost the entire lateral aspect of the caudal peduncle have a dusky overlay; however, as the scales in these regions have light blue-grey centres, the overall coloration varies from blue-black to dark grey. Arising from the dark ventral colour of the belly and chest are 4 broad, dark stripes, lanceolate in outline, with the taper beginning just below the level of the upper lateral line; from this point dorsally, the stripe narrows rapidly and becomes much less definite until it disappears immediately below the dorsal fin base. The first stripe passes over the axil of the pectoral fin; above this point it meets a broad vertical dark stripe on the posterior margin of the operculum. The last body stripe may barely be distinguishable from the dark ground colour of the caudal peduncle. The ground colour of the body between the stripes is light, much lighter than that of the dorsal body surface.

The area of the operculum not covered by the dark posterior band is silvery. The horizontal limb of the preoperculum is blue-black or brownish, the ventral limb

covered by a broad and short dark bar which expands anteriorly onto the cheek. A wide and intense lachrymal stripe extends through the eye onto the nape; the stripes from each side are narrowly separated medially above the orbit. Two distinct, narrow, parallel bands cross the snout anterior to the orbit. In some specimens the lower jaw is blackish, in others it is brownish; the colour is correlated with that of the branchiostegal membrane which may be entirely black or pale with just the posterior (i.e. opercular) part black.

The dorsal fin is yellowish to greyish darkest basally, and with black lappets. Caudal dark basally (the extent variable and its outline irregular), hyaline distally. Anal dark (almost dusky) along the proximal half, yellowish distally, the ocelli large and dead-white. Pelvic fins are black.

Female coloration is unknown.

Ecology. The 6 known specimens came from a trawl haul near Mwama island. Because this particular haul was made over both hard (rock and shingle) and soft (mud) substrates, and at depths from 70–200 feet, little can be said about the habitat of *H. cinctus*.

Only one fish contains ingested material in the gut; the stomach and intestine are filled with colonial blue-green algae, diatoms and other algaecious material. Only the diatoms show signs of digestion. Since the intestine of *H. cinctus* is long and coiled, it is reasonable to assume that the species feeds principally on plant matter.

The 6 male fishes (76.0–87.5 mm. S.L.) on which this description is based, are all adults and are sexually active.

Diagnosis and affinities. In all morphological characters, except male coloration, *H. cinctus* is indistinguishable from *H. paropius*. Yet, in both live and preserved coloration, males of the two species are immediately distinguishable; regrettably no females of *H. cinctus* are available for comparison.

Live fishes differ in obvious and subtle ways (compare p. 17 above with p. 13). Among the obvious differences may be cited the grey-orange head coloration of *H. cinctus* compared with the deep red of *H. paropius*; the clear-cut transverse barring on the flanks of *H. cinctus*, the bars arising from a deep blue-black chest and belly, compared with the silver belly and very faint (or more usually, invisible) bars in *H. paropius*; and finally, the red branchiostegal membrane of *H. paropius* compared with the dusky membrane in *H. cinctus*.

The most obvious interspecific differences in preserved coloration are the dark chest and belly of *H. cinctus*, and the distinct, dorsally incomplete bars on the flanks. No specimen of *H. paropius* has a dark chest and belly (despite the dark margin to the scales in that region) and even in those specimens with bars on the flanks, the bars are much fainter.

These differences may not seem impressive in print but are striking when specimens (especially live fishes) are compared.

Because of the close similarity between *H. cinctus* and *H. paropius*, the comparison of that species with others resembling it can be applied to *H. cinctus* as well (see p. 14). *Haplochromis cinctus* and *H. paropius* are clearly derived from the same stem, and possibly even from the same ancestral species.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.13 (Holotype)	Near Mwama island . . .	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.14-18	Near Mwama island . . .	E.A.F.F.R.O.

Haplochromis erythrocephalus sp. nov

(Text-figs. 9-11)

HOLOTYPE: an adult male, 74.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.251) from the Buvuma channel, south of Ramafuta island.

The trivial name refers to the bright red colour of the head in adult males.

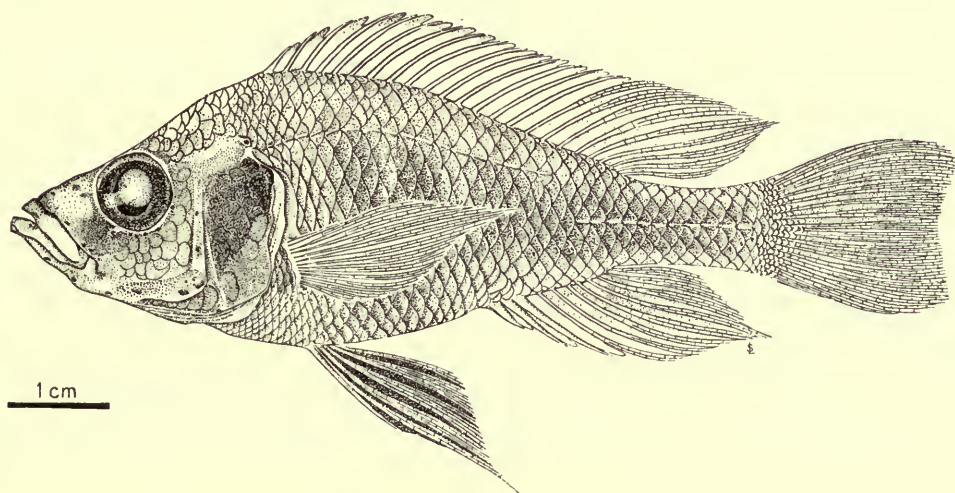


FIG. 9. *Haplochromis erythrocephalus*. Holotype. Drawn by Sharon Lesure.

DESCRIPTION: based on 41 specimens (including the holotype) 58.0-77.0 mm. S.L. Depth of body 34.5-41.5 ($M = 37.1$) % of standard length, length of head 30.4-35.8 ($M = 33.1$) %.

Dorsal head profile with a gentle concavity above the eye, sloping fairly steeply at an angle of 30°-40°.

Preorbital depth 13.6-17.4 ($M = 15.8$) % of head, least interorbital width 22.7-27.9 ($M = 24.6$) %. Snout 1.0-1.2 (mode 1.1) times as broad as long, its length 27.0-32.5 ($M = 29.3$) % of head, diameter of eye 28.6-35.0 ($M = 31.2$), depth of cheek 17.7-23.8 ($M = 20.8$) %.

Caudal peduncle 15.1-20.0 ($M = 17.9$) % of standard length, 1.3-2.0 times as long as deep. These data were obtained from specimens collected at 3 different localities, and it seems possible that there are population differences in the relative depth of the caudal peduncle. Fishes from 2 localities (Buvuma Channel south of

Ramafuta island, and off Bonga Point at the entrance to Pilkington Bay) have shallower peduncles (i.e. more are in the range 1.8–2.0 times as long as deep) than those from Pilkington Bay itself (predominantly in the range 1.5–1.6 times). It must be noted, however, that the samples from Bonga Point ($N = 9$) and Buvuma Channel ($N = 11$) are smaller than that from Pilkington Bay ($N = 21$).

Mouth oblique, sloping at an angle of 30° – 35° (occasionally as steeply as 40°). Jaws equal anteriorly; length of lower jaw 40.2–46.8 ($M = 43.6$) % of head, 1.9–2.6 (mode 2.0) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior orbital margin, occasionally a little posterior to this point.

Gill rakers: 10 (rare)–13, mode 12, on the lower part of the first arch. Lower 1–3 rakers reduced, upper 1–4 usually flattened, often branched, with the uppermost 1 or 2 anvil-shaped; intervening rakers simple, from relatively stout to slender. In a few specimens none of the upper rakers is flattened, the entire series (except the lower part) composed of unbranched, stout to slender rakers.

Scales: ctenoid; lateral line with 30 (f.1), 31 (f.10), 32 (f.20) or 33 (f.7) scales, cheek with 3 (rarely 2) rows. Five (rare) to 7 (rare), mode 6, scales between the upper lateral line and the dorsal fin origin, 5–7 (modal range 6–7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.5), 24 (f.21), 25 (f.14) or 26 (f.1) rays, comprising 15 (f.22) or 16 (f.19) spines and 8 (f.13), 9 (f.23) or 10 (f.5) branched rays. Anal with 10 (f.1), 11 (f.20), 12 (f.18) or 13 (f.2) rays, comprising 3 spinous and 7–10 branched rays. Pectoral 24.6–34.8 ($M = 31.0$) % of standard length. Pelvics with the first ray produced in both sexes; too few females are available to check on possible sexual dimorphism in relative elongation. Caudal truncate or slightly emarginate, scaled on its proximal half.

Teeth. Except posteriorly (and to a certain extent posterolaterally) the *outer teeth* in *both jaws* are mostly somewhat compressed and unequally bicuspid (Text-fig. 10). In some individuals the major cusp tends to be obliquely truncate (rather than almost equilateral in outline).



FIG. 10. *Haplochromis erythrocephalus*. Upper jaw teeth (anterior view), showing variation in crown shape. Scale equals 0.5 mm.

The *posterior upper* teeth are either unicuspid or tricuspid, and are markedly smaller than the anterior and lateral teeth; furthermore, these posterior teeth are deeply embedded in gum tissue and are partly hidden by a fold of the lip. The *posterior lower* teeth do not show such a marked size discrepancy, are usually bicuspid (but with cusps of almost equal size) and are exposed.

There are 42–70 ($M = 56$) outer teeth in the upper jaw.

All *inner teeth* are tricuspid and compressed, implanted more or less vertically, and are arranged in 2 (rarely 1) rows in the upper jaw and a single (less frequently double) row in the lower jaw.

Osteology. The *neurocranium* of *H. erythrocephalus* is essentially similar to that of *H. empodisma* (see fig. 5, in Greenwood, 1956 [the species was then wrongly identified as *H. michaeli*, see Greenwood, 1960, p. 265]). Thus it differs from the neurocranial type found in such species as *H. macrops*, *H. brownae* and *H. nubilus*, species whose syncranial architecture is thought to be of a generalized type. Parenthetically it can be noted that similar generalized neurocrania are found in species like *H. obliquidens* and *H. phytophagus* which have a specialized dentition and feeding habits (see Greenwood, 1956 and 1966).

The skull of *H. erythrocephalus* departs from the generalized type in having a flat, moderately steep dorsal profile (compared with a curved and steep profile), relatively narrower interorbital and otic regions, and a rather more elongate and narrower preorbital part of the skull.

The *dentary* also resembles the *H. empodisma* type in being relatively more slender and elongate than the generalized type.

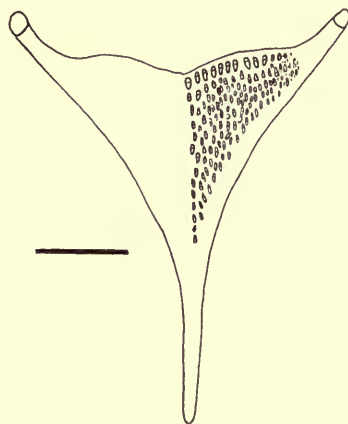


FIG. 11. *Haplochromis erythrocephalus*. Lower pharyngeal bone. Scale equals 2 mm.

The *lower pharyngeal bone* is fine, its triangular dentigerous surface 1.1–1.3 times as broad as long (Text-fig. 11). The teeth are slender, compressed and cuspidate, and are arranged densely but irregularly in from 40–46 rows.

Coloration in life. *Adult males:* The dorsal aspects of the head are bright red, the red pigment extending onto the dorsal part of the body where it becomes fainter and takes on the appearance of a red flush. Body coloration yellowish with a silvery overlay on the flanks and belly.

The dorsal fin is pinkish-red, the caudal has a red flush on its dorsal half with the remainder yellowish to hyaline; anal fin hyaline, with 2 or 3 orange ocelli. Pelvic fins are black.

The live colours of *females* have not been recorded.

Preserved material. *Adult males:* ground colour light fawn to yellowish, a faint purplish-grey area extends over most of the caudal peduncle and then anteriorly as a narrow band or a series of blotches situated midlaterally on the flanks. In some specimens the belly is dusky, and scales in that region have a dark margin. The snout and preorbital region are greyish, with faint indications of 2 narrow, dusky transverse bars across the snout; a dusky, near vertical lachrymal bar extends from the lower orbital margin to the angle of the jaws.

All fins except the pelvics are hyaline, the dorsal with dusky lappets, and the central region of the caudal with a dusky zone; the anal ocelli are faint and greyish in colour. The pelvic fins vary from dusky to intense black.

Females are uniformly light straw-yellow except for a grey snout and preorbital region. Dorsal and caudal fins are greyish, the anal and pelvic fins hyaline, the caudal with a dark base.

Ecology. Habitat. The material used in this description came from 3 localities, viz. Pilkington Bay (depth 30–35 feet, over mud), Bonga Point at the entrance to Pilkington Bay (45–60 feet, over mud) and from the Buvuma Channel south of Ramafuta island (90–100 feet, over mud). Personal observations on trawl catches made in other parts of the Buvuma Channel and in the Napoleon Gulf (at depths of 30–100 feet) suggest that *H. erythrocephalus* has a wide distribution in off-shore localities in the northern parts of Lake Victoria.

Food. The guts of 26 fishes from the 3 localities were examined. In all, both the stomach and intestine are packed with colonial blue-green algae, diatoms and smaller quantities of green algae; in some fishes a few fragments of Crustacea and of insect larvae are also present.

The constitution of this ingested material closely resembles that of the organic mud substrate occurring in the areas from which the fishes were collected. Thus, we conclude that *H. erythrocephalus* feeds on the bottom mud. The ingested colonies of blue-green algae show no signs of digestion at any point in the alimentary tract. In contrast, diatoms found in the intestine are all digested, that is, only the frustules remain; diatoms in the stomach, however, are mostly intact. The crustacean and insect remains are fragmentary, irrespective of their locality in the gut, and consist only of the chitinous parts.

The stomach of *H. erythrocephalus* is large and distensible, the intestine long and coiled.

Breeding. With one possible exception (a male 64 mm. S.L.), all the specimens examined are adult (size range 58–77 mm. S.L.) and most are males. This bias is undoubtedly due to collectors selecting the brilliantly coloured male fishes: it cannot be used to draw any inferences about the distribution or relative abundance of the sexes.

One female (73 mm. S.L., from Bonga Point) with quiescent ovaries, has a few larvae in the buccal cavity, and was probably brooding young at the time of capture.

Too few females have been examined to decide whether or not there is any tendency for asymmetrical ovarian development. However, in some the right ovary is distinctly larger than the left one.

Diagnosis and affinities. Any attempt to analyse the affinities of *H. erythrocephalus* is limited by the existence of superficially similar but as yet undescribed species. For instance, we have under study at the moment four such species, and undoubtedly others will be found as more fishing is carried out in the deep, off-shore waters of the lake.

The four species mentioned above, however, can be distinguished from *H. erythrocephalus* on certain morphometric characters, and in life by differences in male coloration.

Haplochromis erythrocephalus does not seem to be closely related to any of the known in-shore species having small-sized adults with generalized, bicuspid outer teeth. From these species, *H. erythrocephalus* is distinguished by its coloration, longer lower jaw and, with respect to many species, its narrower interorbital width and higher gill raker count. The oblique lower jaw of *H. erythrocephalus* also serves as a diagnostic feature.

The oblique mouth, high gill raker count, the broader, more densely toothed lower pharyngeal bone, and the long intestine serve to separate *H. erythrocephalus* from *H. empodisma* juveniles of a comparable length. (*H. empodisma* occurs in some of the shallower localities from which *H. erythrocephalus* has been recorded.) In a earlier paper, Greenwood (1960) was referring to *H. erythrocephalus* when he wrote "... The nearest living relative of *H. empodisma* is a small and as yet undescribed species which occurs in the same habitat but is confined to shallow water". The latter part of this statement now requires correction (both species occur in deep water). For the moment, the first part still seems valid, particularly if the strength of the term "nearest relative" is diluted a little to read "A near relative ...".

Of the known (and described) species from deeper water habitats, *H. erythrocephalus* bears some superficial resemblance to *H. paropius*, including red pigment on the head of adult males. This red coloration in *H. paropius* is, however, much darker, and there are other colour differences (cf. p. 21 above with p. 13). Certain anatomical differences may also be noted, viz. the higher gill raker count in *H. erythrocephalus* (11-13, mode 12, cf. 8-10, mode 9), the concave head profile of *H. erythrocephalus* (gently convex or nearly straight in *H. paropius*) and differences in the morphology of the neurocranium (cf. pp. 21 and 12).

Haplochromis paropius, like *H. erythrocephalus*, is probably not an isolated species since we have evidence of an *H. paropius* species complex. But, the diagnostic characters for *H. paropius* also serve to separate the other related species from *H. erythrocephalus*.

The neurocranium of *H. erythrocephalus* is of interest. Its shape and proportions are unlike those characterizing the skulls of other species with small-sized adults, a generalized body-form and unspecialized dentition (or even specialized grazing or browsing teeth). Instead, it closely approximates to the neurocranial form found in *H. empodisma*, trophically a generalized bottom-feeding species with an unspecialized dentition but one with larger sized adults.

The significance of these differences or resemblances in neurocranial form (and correlated characters in the syncranial skeleton) are difficult to evaluate. They may suggest that *H. erythrocephalus* was derived from a different stem than that for

many of the other *Haplochromis* species with small-sized adults and a generally unspecialized anatomy (including those new species described in this paper).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.251 (Holotype)	Buvuma Channel, S. of Ramafuta isl. (90-100 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.270-291	Pilkington Bay	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.262-269	Bonga Point (mouth of Pilkington Bay)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.252-261	Buvuma Channel, N.W. of Vuga isl. (90-100 feet)	E.A.F.F.R.O.

Haplochromis melichrous sp. nov.

(Text-figs. 12-15)

HOLOTYPE: an adult male 98.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.150) from a trawl haul made between Nsadzi island and the mainland.

The trivial name (from the Greek for honey-coloured) refers to the golden-brown coloration of female fishes.

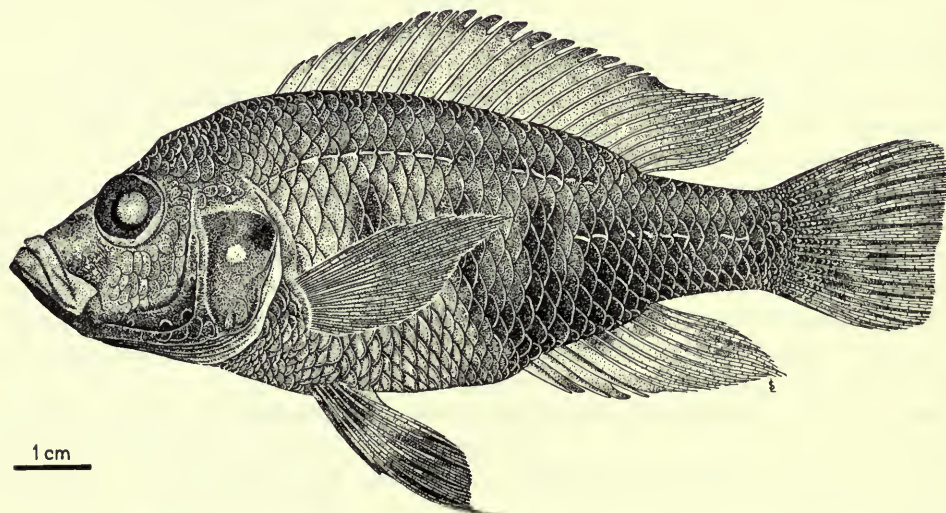


FIG. 12. *Haplochromis melichrous*. Holotype. Drawn by Sharon Lesure.

DESCRIPTION: based on 18 specimens (including the holotype) 69.0-107.0 mm. S.L.

Depth of body 36.5-44.5 ($M = 39.9$) % of standard length, length of head 34.2-36.1 ($M = 34.9$) %.

Dorsal head profile concave (strongly so in some fishes), sloping at an angle of 30°-35°. Premaxillary pedicels not prominent. Pores of the cephalic lateral line system enlarged, the tubes and pores on the preorbital being especially prominent.

Preorbital depth 14.6–18.6 ($M = 16.4$) % of head, least interorbital width 18.6–23.6 ($M = 22.1$) %. Snout broader than long (1.1–1.3, mode 1.3, times), its length 27.0–33.3 ($M = 31.1$) % of head; eye diameter 24.5–29.8 ($M = 27.6$), depth of cheek 21.7–28.5 ($M = 25.4$) %.

Caudal peduncle 15.0–19.4 ($M = 17.6$) % of standard length, 1.1 (rare)–1.7 (mode 1.3) times as long as deep.

Mouth oblique, sloping at an angle of 35°–40°; lower jaw projecting, with the tip lying above the tip of the premaxilla (rarely with the jaws equal anteriorly). Length of lower jaw 44.7–48.8 ($M = 46.9$) % of head, 1.5–2.0 (modal range 1.8–1.9) times its breadth; a distinct mental protuberance is developed in most specimens. Posterior extension of the maxilla variable, from a point reaching a vertical slightly anterior to the orbit, to one passing through the anterior part of the eye.

Gill rakers: 9 or 10 on the lower part of the first arch, the lower 1–3 rakers reduced, the upper 3 or 4 flattened (some lobed, other anvil-shaped), and the intervening rakers either short and stout or relatively slender.

Scales: ctenoid. Lateral line with 30 (f.3), 31 (f.10) or 32 (f.4) scales, cheek with 3 or 4 rows. Five to 7 (mode 6½) scales between the upper lateral line and the dorsal fin origin, 5 or 6 (mode), rarely 7, between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.12), 24 (f.5) or 25 (f.1) rays, comprising 14 (f.2) or 15 (f.16) spines and 8 (f.11), 9 (f.5), or 10 (f.2) branched rays. Anal with 11 (f.15) or 12 (f.3) rays, comprising 3 spines and 8 or 9 branched elements. Pectoral fin 28.5–33.3 ($M = 30.8$) % of standard length. Caudal truncate or obliquely truncate (i.e. the lower posterior margin slopes forwards and downwards), scaled on its proximal half. Pelvics with the first 2 rays produced (the first ray longer) in both sexes but proportionately more so in adult males.

Teeth. In the *outer row of both jaws* there is an admixture of slender, somewhat compressed bicuspid, weakly bicuspid, and unicuspid (Text-fig. 13); the relative proportions of the different types shows great individual variability. Teeth situated laterally and posterolaterally in the premaxilla are strongly incurved, and in most specimens the posterolateral teeth are enlarged. The posterolateral and posterior teeth in the lower jaw are often tricuspid and small. There are 56–80 ($M = 68$) outer teeth in the upper jaw.

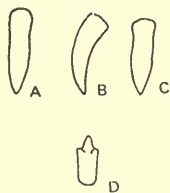


FIG. 13. *Haplochromis melichrous*. A–C upper jaw teeth. A and C: in anterior view. B: in lateral view. D: tricuspid tooth from the lower jaw. Scale equals 1 mm.

The *inner teeth* are tricuspid (sometimes weakly so) and are very obliquely implanted so as to lie almost horizontally. There are 2 (rarely 3) series of inner teeth in the upper jaw, and 2 (rarely 1) in the lower jaw.

Osteology: The *neurocranium* of *H. melichrous* (Text-fig. 14) resembles that of *H. victorianus*; in other words it is referable to the "*serranus*" group (see Greenwood, 1967, p. 109). It differs from the neurocranium of *H. victorianus*, however, in having a narrower and more acute preorbital region.

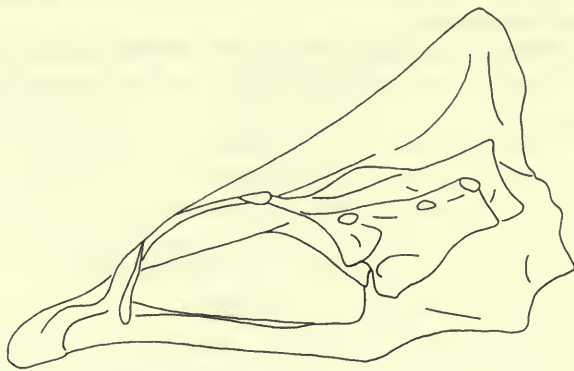


FIG. 14. *Haplochromis melichrous*. Neurocranium in left lateral view. Scale equals 2 mm.

The *premaxilla* is slightly expanded medially and anteromedially, and its lateral and posterolateral teeth are strongly incurved.

The *dentary* has a strong mental protuberance; although the openings into the lateral line tubes are enlarged, the tubes themselves are not hypertrophied.

The dentigerous surface of the *lower pharyngeal bone* is as broad as long, or slightly broader (Text-fig. 15). The teeth are fine, and arranged in from 30–34 rows; apart

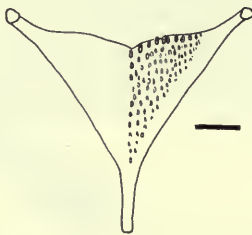


FIG. 15. *Haplochromis melichrous*. Lower pharyngeal bone. Scale equals 2 mm.

from the posterior pair of teeth in the median row, no others in this row are noticeably coarser than the lateral teeth.

Coloration in life. *Males* have a dark ground colour but with lighter, faintly iridescent greyish patches on the flanks, and sometimes three faint transverse bars on the anterior flanks. The dorsal fin is hyaline with dark lappets, the caudal hyaline and faintly maculate. The anal fin is dusky at its base and hyaline or faintly red distally; the ocelli are large and orange. Pelvic fins are black.

Females are dark golden-brown on the dorsal aspects of the body and on the flanks, shading to silver ventrally; a faint, dark midlateral stripe is generally visible. The dorsal fin is faintly golden-brown proximally. The pelvics are hyaline.

Preserved material. *Males*: have a yellow-brown ground coloration. The chest region is silvery but the scales here (and on the belly) are edged with black. The snout, lower jaw, branchiostegal membrane, lower part of the preoperculum, the entire interoperculum and most of the ventral aspects of the operculum are dusky. The ventral half to two-thirds of the body posterior to the vent is also dusky; 3-5 broad but relatively faint vertical bars originate from this dark area, and extend upwards to the level of the upper lateral line or slightly higher (but never to the dorsal body outline).

Dorsal fin dark grey to dusky, the lappets black. Caudal fin greyish to dusky, darkest basally, and maculate distally. The anal fin is dusky distally, black basally and over the spinous part; the ocelli are whiteish but very indistinct. The pelvic fins are black.

The smallest male examined (74 mm. S.L., adult but apparently quiescent) has the overall tone of the ventral body half much lighter than in the other specimens, but the margins of the scales in this region are very dark.

Females are greyish-yellow above the midlateral line, light yellow-brown below, with a faint silver overlay on the chest region. Most specimens have a faint but broad midlateral stripe, interrupted at about its mid-point for a variable distance; sometimes only a short (i.e. about 5 scale rows long) anterior part of this stripe is detectable. The tip of the lower jaw is dusky, and there is a short, rather indistinct lachrymal stripe which does not reach the ventral margin of the preoperculum. The dorsal and caudal fins are greyish, the latter sometimes maculate but always with the proximal part darkest. Anal and pelvic fins are hyaline.

Ecology. Habitat. The specimens described above came from trawl hauls made in water 70-100 feet deep, over a mud bottom between Nsadzi island and the mainland. One of us (J.M.G.) has identified *H. melichrous* in catches made south of this island over a similar bottom but at depths of from 130-160 feet.

Food. Little information could be gathered from the 10 guts examined. Most were almost empty save for small quantities of mud and fragments of crustaceans (probably *Caridina* sp); other fragments (taken from 3 guts) were tentatively identified as being remains of pupal Diptera.

Breeding. All except one of the specimens available (69-107 mm. S.L.) are adults; the smallest fish is a juvenile female, but the ovaries show early signs of oogenesis. The next smallest fish (74 mm. S.L.), a male, is adult. In all 8 adult and sexually active females, the right ovary is noticeably larger than the left one.

Diagnosis and affinities. The concave dorsal head profile, the oblique lower jaw, broad snout, and the colours of live fishes serve to distinguish *H. melichrous* from any of the deep water *Haplochromis* species so far discovered.

Haplochromis melichrous does not closely resemble any of the known inshore and shallow water species; it is readily distinguished from such oblique-mouthed species as *H. cavirostris*, *H. plagiostoma*, *H. flavipinnis* and certain extreme forms of

H. obesus (see fig. 2 and p. 183 in Greenwood, 1959) by several morphometric and dental characters.

There are few pointers to the phyletic affinities of *H. melichrous*. Judging from the dentition and syncranial architecture, the species could be associated with the "*serranus*" group (see Greenwood [1967], page 109, *et seq.*) as a rather specialized off-shoot. Equally, it could be associated with the *H. flavipinnis*-*H. cavifrons* group, a species complex of uncertain affinities but one probably related (at least in part) to the "*serranus*" group.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.150 (Holotype)	Between Nsadzi isl. and mainland (70-100 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.151-167	Between Nsadzi isl. and mainland (70-100 feet)	E.A.F.F.R.O.

Haplochromis laparogramma sp. nov.

(Text-figs. 16-19)

HOLOTYPE: an adult male 78.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.220) from north of Nsadzi island.

The trivial name refers to the conspicuous midlateral stripe.

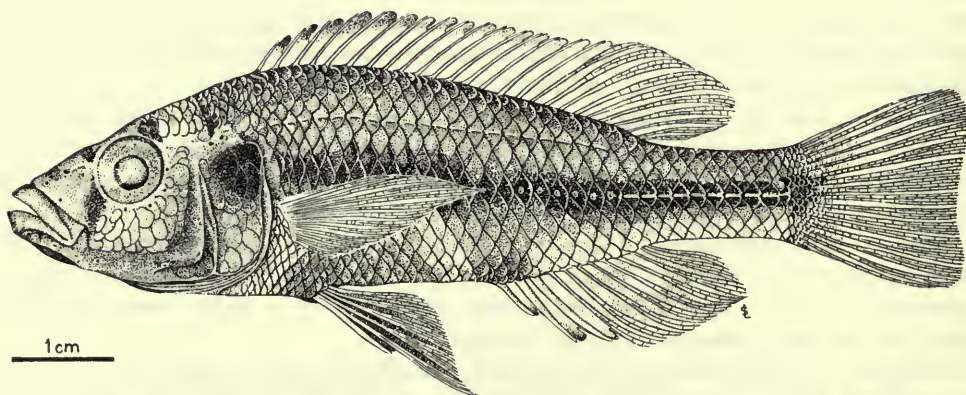


FIG. 16. *Haplochromis laparogramma*. Holotype. Drawn by Sharon Lesure.

DESCRIPTION: based on 25 specimens (including the holotype), 61.0-84.5 mm. S.L.

Depth of body 27.5-31.1 ($M = 29.3$) % of standard length, length of head 30.1-33.8 ($M = 30.5$) %.

Dorsal head profile straight or slightly curved in the nuchal region, sloping at an angle of 25°-30°.

Preorbital depth 14.6–18.8 ($M = 16.3$) % of head, least interorbital width 24.0–27.0 ($M = 25.7$) %. Snout as long as broad to 1.3 times broader than long (mode 1.1 times), its length 27.4–31.9 ($M = 30.2$) % of head, eye diameter 26.7–32.6 ($M = 30.0$), depth of cheek 15.8–21.3 ($M = 19.5$) %.

Caudal peduncle 17.7–22.0 ($M = 20.0$) % of standard length, 1.7–2.1 (modal range 1.8–1.9) times as long as deep.

Lower jaw sloping fairly steeply at an angle of 25° – 35° (less frequently at *ca.* 20°), its length 40.7–45.4 ($M = 42.8$) % of head, and 1.8–2.6 (mode 2.2) times its breadth. Jaws equal anteriorly or the lower projecting slightly, terminating in a low mental protuberance. Posterior extension of the maxilla variable, from a point slightly anterior to the orbital margin to one below the anterior part of the eye.

Gill rakers: 11 (mode) or 12, rarely 10 or 13, on the lower part of the first gill arch. The lower 1–4 rakers are reduced, the upper 2–5 flattened, sometimes branched and often anvil-shaped; intervening rakers are relatively slender.

Scales: ctenoid; lateral line with 32 (f.4), 33 (f.10), 34 (f.6) or 35 (f.2) scales, cheek with 3 (rarely 2 or 4) rows. Five and a half or 6 scales between the upper lateral line and the dorsal fin origin, 5–6 (mode) rarely 7, between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.10), 25 (f.14) or 26 (f.1) rays, comprising 15 (f.18) or 16 (f.7) spines and 9 (f.16) or 10 (f.9) branched rays. Anal with 11 (f.10) or 12 (f.15) rays, comprising 3 spines and 8 or 9 branched rays. Pectoral 24.4–30.1 ($M = 27.7$) % of standard length. Pelvics with the first ray produced in both sexes. Caudal truncate, scaled on its basal half.

Teeth. Except posteriorly in both jaws, the *outer* teeth are compressed and unequally bicuspid (Text-fig. 17); in a few specimens there are tricuspid, compressed

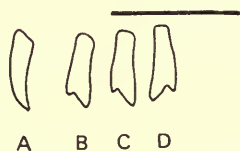


FIG. 17. *Haplochromis laparogramma*. Upper jaw teeth, all from one fish, to show variation in crown shape. A: lateral view. B–D: anterior view. Scale equals 2 mm.

teeth interspersed among the bicuspid. Most individuals have weakly bicuspid or unicuspid, or (less commonly) tricuspid teeth posteriorly in the upper jaw, and tricuspid in the same position in the lower jaw. Exceptionally, there are bicuspid teeth throughout the outer row. In both jaws the posterior teeth are smaller than the anterior and lateral ones. Not infrequently the posterior quarter of the pre-maxilla is edentulous.

There are 46–62 ($M = 54$) outer teeth in the upper jaw.

The *inner teeth* are tricuspid, and are arranged in 2 (less commonly 3) series in the upper jaw and 1 or 2 series in the lower jaw.

Osteology. The *neurocranium* is close to a generalized type (see Greenwood, 1962) but shows certain specializations, such as the rather more protracted preorbital

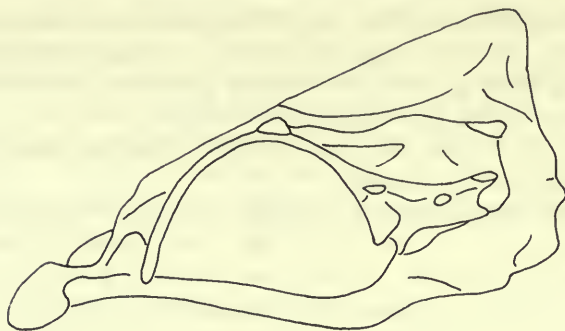


FIG. 18. *Haplochromis laparogramma*. Neurocranium in left lateral view. Scale equals 2 mm.

region which is also less steeply sloping and is straighter (Text-fig. 18). Also, the otic region is narrower than in the generalized type (greatest breadth contained *ca.* 2 times in neurocranial length *cf.* $1\frac{1}{2}$ times).

Broadly speaking, the neurocranium of *H. laparogramma* can be considered intermediate between the *H. brownae* type and the *H. serranus* type (see Greenwood, *op. cit.*).

Lateral line canals on the neurocranium are not enlarged, and neither are those on the dentary; the canals on the preorbital bone, however, are slightly enlarged.

The *dentary* departs slightly from the generalized type since it is relatively elongate. The *premaxilla* shows the development of a slight beak through the expansion of its anterior and anterolateral dentigerous surfaces.

The *lower pharyngeal bone* is slender and rather narrow (Text-fig. 19). Its dentigerous surface is as long as broad, and carries 32–38 rows of slender, cuspidate teeth.

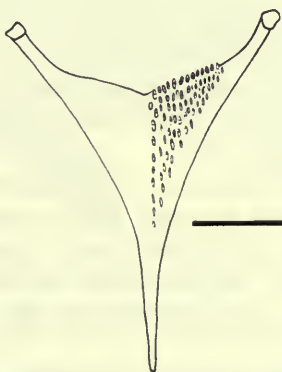


FIG. 19. *Haplochromis laparogramma*. Lower pharyngeal bone. Scale equals 2 mm.

Coloration in life. Adult males have the dorsal part of the body dark blue, shading to greenish-silver on the flanks, and silver on the belly. A dark midlateral stripe

runs from behind the head to the origin of the caudal fin. Dorsal aspects of the head vary from brownish to yellowish-brown; the snout is sometimes crossed by 2 distinct dark bars which are weakly chevron-shaped, the apex directed orally. The opercular region and the cheek are yellowish, but the branchiostegal membrane is dusky. The dorsal and caudal fins are pale yellowish-orange, the anal is hyaline with orange ocelli. Pelvic fins are black.

Live coloration for *females* is unknown.

Preserved coloration. *Males*: are light to dark brown on the dorsal half of the body and caudal peduncle, silvery below, with a faint duskiness on the chest, belly and, in some specimens, the flanks as well. The brown and silver colours are distinctly demarcated by a broad midlateral stripe extending from behind the operculum to the caudal origin. This stripe is of variable thickness, being broadest over the anterior two-thirds of its length. The snout is dusky, with faint traces of 2 darker transverse bars, the upper of which is interocular in position; in some fishes the occiput is also dusky. In all specimens there is a faint but broad lachrymal stripe, and in some a faint prolongation of the midlateral band across the operculum to the vertical preopercular limb. The branchiostegal membrane is dusky.

Dorsal and anal fins are hyaline, with faintly dusky lappets; the anal ocelli are dead-white. The caudal fin is also hyaline but becomes darker near the base. The pelvic fins vary from dusky to black.

The preserved coloration of *females* is similar to that of males but lacks the ventral duskiness on the chest, belly and flanks.

Ecology. Habitat. The species has been recorded from 4 off-shore localities. In all, the bottom was of mud, and the depth varied from 50–110 feet. *Haplochromis laparogramma* has not yet been identified from catches made in deeper water.

Food. The guts of 20 individuals from 3 different localities have been examined. Apart from 5 empty guts, all contained varying amounts of fragmentary larval and pupal Diptera. In none was any bottom detritus recorded, thus suggesting that *H. laparogramma* does not feed directly on the bottom.

Breeding. All the specimens available (61–85 mm. S.L.) are adults; in the 3 females examined, the right ovary is clearly larger than the left one, the discrepancy being most marked in the single "ripe" individual.

Diagnosis and affinities. For the moment it is difficult to suggest the relationships of *H. laparogramma*, but this may become simpler when more is known about the *Haplochromis* species from deeper water habitats. Certainly *H. laparogramma* cannot be closely associated with any of the known inshore species having a similar general facies, as for example, *H. longirostris* (see Greenwood, 1962).

Among the deep water "trawl species", *H. laparogramma* may be related to *H. fusiformis* (see p. 32). Superficially *H. laparogramma* is distinguished by its coloration, slightly broader snout, larger eye (possibly correlated with the smaller adult size of the species), coarser teeth, larger scales on the nape, and its smaller adult size.

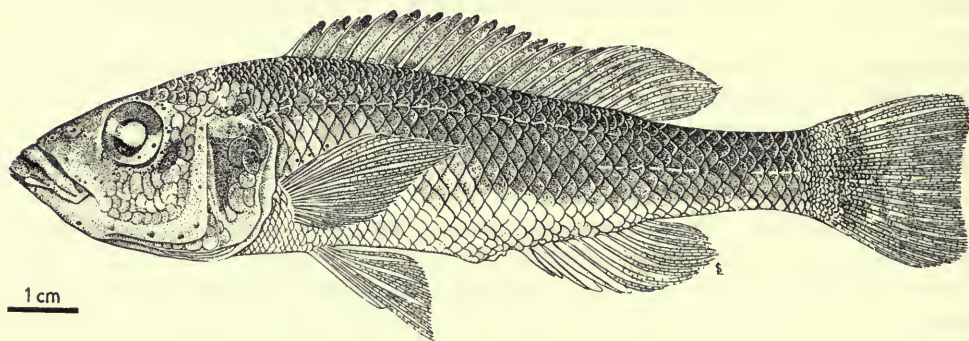
STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.220 (Holotype)	N. of Nsadzi isl. (70-100 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.233-239	Buvuma Channel, W. of Vuga isl. (108 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.39.240-251	Off the Bulago-Tavu bank (50- 75 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.221-232	N. of Nsandzi isl. (70-100 feet)	E.A.F.F.R.O.

Haplochromis fusiformis sp. nov.

(Text-fig. 20)

HOLOTYPE: an adult female 110.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.28) from the Buvuma Channel, west of Nienda and Vuga islands, at a depth of 108 feet. The trivial name refers to the slender, elongate body form of this species.

FIG. 20. *Haplochromis fusiformis*. Holotype. Drawn by Sharon Lesure.

DESCRIPTION: based on 10 specimens (including the holotype) 74.5-110.0 mm. S.L.

Depth of body 23.2-25.5 ($M = 24.6$) % of standard length, length of head 30.4-32.1 ($M = 31.3$) %. Dorsal head profile slightly curved, sloping at an angle of about 30°, its outline broken by the fairly prominent premaxillary pedicels. The openings to the cephalic lateral line system are not noticeably enlarged.

Preorbital depth 15.7-19.3 ($M = 17.4$) % of head, least interorbital width 21.9-26.0 ($M = 24.5$) %. Snout 1.0-1.2 (mode 1.1) times as long as broad, its length 29.4-34.4 ($M = 31.9$) % of head, eye diameter 23.4-27.7 ($M = 26.3$), depth of cheek 15.4-21.4 ($M = 18.9$) %.

Caudal peduncle 18.6-21.4 ($M = 20.0$) % of standard length, 1.9-2.1 (modal range 2.0-2.1) times as long as deep.

Lower jaw sloping at an angle of ca. 20°-30°, jaws equal anteriorly or the lower projecting slightly, its length 40.4-43.8 ($M = 42.2$) % of head, and 2.0-2.6 (no distinct mode) times its breadth. Posterior tip of the maxilla reaching a vertical

slightly anterior to the orbital margin, or more posteriorly to one through the orbital margin.

Gill rakers: ten or 11 on the lower part of the first arch, the lower 1-3 rakers reduced, the upper 2-5 flattened and branched; intervening rakers are relatively slender.

Scales: ctenoid; lateral line with 34 (f.2), 35 (f.3), 36 (f.2) or 37 (f.1) scales, cheek with 3 or 4 rows. Seven or 8 (rarely 6) between the dorsal fin origin and the upper lateral line, 5 or 6 (mode) between the pectoral and pelvic fin bases.

Fins. Dorsal with 25 (f.2) or 26 (f.8) rays, comprising 15 (f.2), 16 (f.7) or 17 (f.1) spines and 9 (f.2), 10 (f.7) or 11 (f.1) branched rays. Anal with 11 (f.4), 12 (f.5) or 13 (f.1) rays, comprising 3 spines and 8-10 branched rays. Pectoral 23.1-27.0 ($M = 25.1$) % of standard length. Caudal truncate (obliquely so in 2 specimens), scaled on its proximal half to three-fifths. Pelvics with the first ray slightly produced in both sexes, but relatively more so in males.

Teeth. Slender but compressed, unequally bicuspid teeth predominate in the outer row of both jaws in almost all specimens, but the posterior teeth in the lower jaw are generally tricuspid or weakly tricuspid. Some weakly bicuspid, or unicuspid teeth occur anteriorly in both jaws.

Two exceptional specimens have mostly unicuspid teeth laterally and anteriorly in both jaws, with a few bicuspid teeth interspersed.

There are 44-64 outer teeth in the upper jaw; the 2 largest specimens have the lowest number of teeth (44 and 48), an unusual inverse correlation.

In most specimens the posterior quarter of the premaxilla is edentulous, but in a few the bone is toothed along its entire length.

The *inner rows* are composed of tricuspid or weakly tricuspid teeth arranged in 2 (mode) or 3 series in the upper jaw and 1 or 2 series in the lower jaw.

Osteology. No complete skeleton is available. The *lower pharyngeal bone* is fine, its denticerous surface 1.1-1.2 times as broad as long, and carries 34-36 rows of slender, weakly cuspidate teeth.

Coloration of live fishes. *Males* have the dorsal part of the body brilliant purple-blue, shading to silvery-yellow on the flanks, and becoming dusky on the ventral surfaces. All fins (except the black pelvics) are dark basally and hyaline distally; the anal has 2 or 3 white ocelli.

Females have the dorsal part of the body blue-grey, shading to silver on the flanks and ventral surfaces. Fins are coloured as in the males, except that the pelvics are hyaline and there are no ocelli on the anal.

Preserved material. *Males* have a dark grey-brown ground coloration, but are sooty on the chest, belly and that area of the ventral body wall above the anterior part of the anal fin (in a few exceptional specimens the chest and belly are yellow). There are no distinct cephalic markings, although in some fishes there are traces of a medially interrupted occipito-nuchal band. The branchiostegal membrane is grey brown.

The dorsal fin is grey to sooty, the lappets black; in most specimens there is a dark but poorly defined band running along the fin base. The anal is grey, darker (nearly black) basally and over the spinous part of the fin. The pelvics are black.

Females are greyish brown dorsally, straw yellow below; the snout and dorsal surface of the head are grey. Except for the usual dark opercular spot, the head is without markings, and the branchiostegal membrane is pale. The dorsal and anal fins are greyish to lightly sooty, the anal and pelvic fins are hyaline.

Ecology. Habitat. The 10 specimens available came from two off-shore areas in the Buvuma Channel. In both places the substrate is mud, the depth 90–96 feet and about 108 feet respectively.

Food. Four of the 9 guts examined were empty. The remainder contained small quantities of unidentifiable insect fragments (probably from pupal Diptera).

Breeding. All 10 fishes are probably adults, although some doubt is felt about the sexual state of one female (93 mm. S.L.); this individual might be a juvenile. Like the three other females, the right ovary in this fish is larger than the left one.

Diagnosis and affinities. The possible relationship between *H. fusiformis* and *H. laparogramma* is mentioned on p. 31, and the features distinguishing the 2 species are listed there. Until more specimens of *H. fusiformis* are available this tentative relationship cannot be explored further. At least for the moment, the slender, elongate body-form coupled with the moderately oblique lower jaw serve to distinguish both species from the other deep-water *Haplochromis* species.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.28 (Holotype)	Buvuma Channel, W. of Nienda and Vuga isls. (108 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.29–38	Buvuma Channel, W. of Nienda and Vuga isls. (108 feet)	E.A.F.F.R.O.

Haplochromis dolichorhynchus sp. nov.

(Text-figs. 21–24)

Haplochromis tridens (part): Greenwood, 1967, *Bull. Br. Mus. nat. Hist. Zool.*, **15**: no. 2, 97.

NOTE ON THE SYNONYMY. A single specimen (B.M. [N.H.] reg. no. 1966.3.9.165) previously identified as *H. tridens* by Greenwood (1967) is now re-identified as *H. dolichorhynchus*. This fish is the aberrantly coloured female noted on p. 99 of that paper.

HOLOTYPE: an adult male 102.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.168) from Murchison Bay, at a depth of 30 feet.

The trivial name refers to the rather protracted snout of this species relative to the snout in its presumed relatives.

DESCRIPTION: based on 27 specimens (including the holotype), 67.5–119.0 mm. S.L.

Depth of body 28.6–33.6 (M = 31.9) % of standard length, length of head 33.4–36.9 (M = 35.5) %.

Dorsal head profile straight to slightly concave, sloping at an angle of 20°–30°; premaxillary pedicels fairly prominent and breaking the outline of the profile to

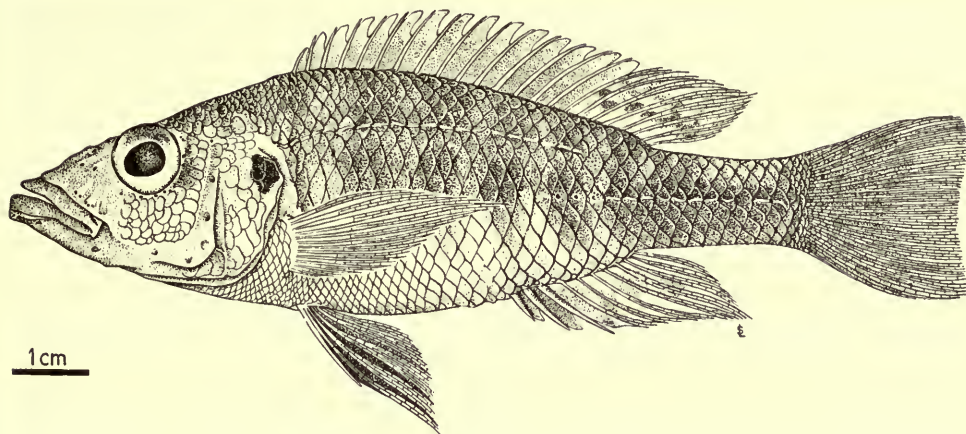


FIG. 21. *Haplochromis dolichorhynchus*. Holotype. Drawn by Sharon Lesure.

create a concavity above and a little anterior to the eye. The cephalic lateral line pores are enlarged and obvious.

Preorbital depth 16.0–19.5 ($M = 17.7$) % of head, least interorbital width 16.3–21.2 ($M = 18.8$) %. Snout 1.0–1.4 (mode 1.1) times as long as broad, its length 30.3–37.7 ($M = 34.2$) % of head. Eye and orbit almost circular, eye diameter 25.0–29.6 ($M = 27.2$) % of head, depth of cheek 16.7–23.0 ($M = 19.6$) %.

Caudal peduncle 17.1–21.4 ($M = 19.2$) % of standard length, 1.6–1.9 (modal range 1.7–1.8) times as long as deep.

Mouth somewhat oblique (*ca.* 15°–25°), lower jaw projecting slightly to strongly (the usual condition), and with a distinct mental protuberance; length of lower jaw 42.8–52.5 ($M = 47.8$) % of head, 2.0–2.8 (mode 2.1) times as long as broad. Premaxilla distinctly expanded medially so as to give it a beaked appearance. Posterior tip of the maxilla reaching a vertical slightly anterior to the orbital margin, occasionally a little posterior to this line.

Gill rakers: 9–11 (mode 10), rarely 8, on the lower part of the first gill arch. The lower 1–4 rakers are reduced, the upper 3 or 4 flattened and usually divided, the intervening rakers of varied form but generally either stout or slender.

Scales: ctenoid. Lateral line with 31 (f.2), 32 (f.5), 33 (f.16) or 34 (f.3) scales. Cheek with 3 (mode) or 4 rows. Five to 6½ (mode 5½) scales between the upper lateral line and the dorsal fin origin, 6 or 7 (mode) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.3), 24 (f.18) or 25 (f.5) rays, comprising 14 (f.1), 15 (f.22) or 16 (f.3) spines and 8 (f.4), 9 (f.18) or 10 (f.4) branched rays. Anal with 11 (f.12) or 12 (f.14) rays, comprising 3 spines and 8 or 9 branched rays. Pectoral 24.5–30.8 ($M = 27.4$) % of standard length. Pelvic fins with the first ray produced, about equally so in both sexes. Caudal truncate, scaled on its proximal half.

Teeth. Except posteriorly, the *outer* teeth in the *upper* jaw are predominantly of a slender, somewhat compressed form, gently curved, with unequally bicuspid crowns (Text-fig. 22); the major cusp is noticeably produced. In many fishes there

are admixtures of bi- and weakly bicuspid teeth, or of bi- and unicuspid (the latter usually situated anteriorly); rarely, some tricuspid, compressed teeth occur anteriorly and laterally in the outer row.

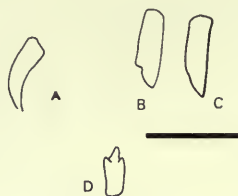


FIG. 22. *Haplochromis dolichorhynchus*. A–C upper jaw teeth. A: in lateral view. B and C: in anterior view. D: posterolateral tooth from the dentary. Scale equals 1 mm.

Posteriorly and posterolaterally it is usual to find tricuspid teeth, but unicuspid and bicuspid are sometimes found in this position, or there can be a combination of unicuspid posteriorly with tricuspid posterolaterally.

There are 50–80 ($M = 70$) teeth in the outer series of the upper jaw.

The *outer row* of teeth in the *lower jaw* is usually like that in the upper jaw; when tricuspid teeth occur posteriorly, they are slightly larger than their counterparts in the upper jaw.

Only tricuspid teeth occur in the obliquely implanted *inner rows*, arranged in 2 or 3 series in the upper jaw, and 1 or 2 in the lower jaw.

Osteology. The *neurocranium* of *H. dolichorhynchus* closely resembles that of *H. prognathus* (see Greenwood, 1967, pp. 81, and 109 *et seq.*) being moderately shallow with a gently sloping anterior dorsal profile, and a fairly elongate preorbital region (Text-fig. 23). The neurocranial lateral line canals and pores, however, are

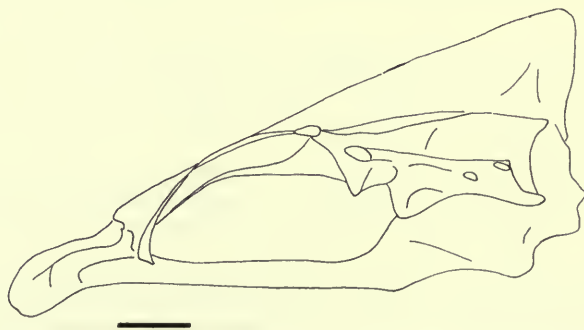


FIG. 23. *Haplochromis dolichorhynchus*. Neurocranium in left lateral view. Scale equals 4 mm.

moderately enlarged, especially when compared with the condition found in previously described species of the "*prognathus*" group (see Greenwood, 1967, *loc. cit.*).

The *premaxilla* has a pronounced beak resulting from the anterior and anterolateral expansion of its dentigerous arm; the pedicels are as long as the dentigerous arms.

The *dentary* has a marked outward flare of its upper half so that when viewed from in front, each ramus has a concave outer face. This flare is continued forward almost to the symphysis. The lower lateral faces of the symphyseal surface are produced forward as a conical mental process.

The *lower pharyngeal bone* (Text-fig. 24) has its dentigerous surface slightly longer than broad or, more frequently, a little broader than long (about 1.1–1.2 times).

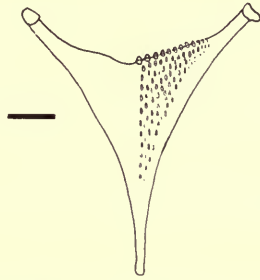


FIG. 24. *Haplochromis dolichorhynchus*. Lower pharyngeal bone. Scale equals 2 mm.

The lower pharyngeal teeth are fine and weakly cuspidate (except posteriorly), and arranged in 28–30 rows.

Coloration in life. *Males* are blueish-purple dorsally, becoming silvery on the flanks; the ventral surfaces are dusky. The lips and branchiostegal membrane are greenish-blue. Dorsal, caudal and anal fins are dark basally, hyaline distally, the dorsal sometimes with red maculae, and the caudal usually maculate; anal ocelli are orange-red. The pelvic fins vary from black to dusky.

Females are blue dorsally, becoming silver on the flanks and belly; the blue coloration is of variable intensity. A dark longitudinal stripe (of variable intensity) runs midlaterally along the entire body length behind the head. All fins are hyaline.

Preserved material. *Males (sexually active)* are brownish above, with the entire ventral half of the body and the lower four-fifths of the peduncle blue-black except for irregular silvery blotches on the flanks above the belly. There are traces of 5, ill-defined, narrow vertical bars stemming from the black ventral body coloration and extending to the dark streak lying along the dorsal fin base; a sixth faint bar is visible on the caudal peduncle. The cheek, branchiostegal membrane and operculum dark, the latter with a silvery sheen; the upper lip and lower jaw are greyish, the lower lip whiteish. A faint but broad band crosses the anterior part of the snout.

The dorsal fin is greyish, with sooty lappets and dark spots at the base of all the rays; the soft part of the fin is darkly maculate. The caudal is dark on its basal third, greyish-sooty distally and darkly maculate on its upper half. The anal dark grey with a deep, sooty basal band which expands in the region of the spines. Pelvic fins black on the proximal three-quarters medially, entirely black laterally.

Males (sexually quiescent) are dark yellow-brown dorsally, becoming darker on the ventral half of the body and caudal peduncle but with a silvery sheen on the chest and, less markedly, the belly. The snout is dark, but the rest of the head is yellowish-

brown; the branchiostegal membrane is sooty. The fins are as in active males, or are much paler.

In some quiescent males faint traces of the vertical black bars are visible on the body, as are the various cephalic markings, including a postocular blotch, and a transverse bar across the snout.

Immature males have the same coloration as females (see below) except that the pelvic fins are dusky.

Females have a silvery-grey ground coloration which shades to yellowish-brown ventrally. A dark, usually interrupted midlateral band runs from behind the head to the proximal quarter of the caudal fin. The margins of this band are irregular, and the band is of variable width; the band is usually interrupted above the anterior part of the anal fin, but if it is complete, it is constricted in this region. In a few specimens the band does not appear on the anterior half of the body. A few small, irregularly placed dark blotches are often present between the upper lateral line and the dorsal fin base.

The dorsal fin is light grey, with faintly dusky lappets, and often has small dark areas at the bases of the spines. Caudal fin greyish, anal and pelvic fins hyaline.

Ecology. Habitat. *Haplochromis dolichorhynchus* has a wide depth range from 30 to more than 100 feet. It has been caught in open off-shore waters and in a relatively sheltered bay. In all localities, the substrate is mud.

Food. The guts of 25 specimens from three different localities were examined. Fishes from greater depths (70–108 feet) had fed on small Crustacea (especially *Caridina* sp.) and, to a lesser degree, on pupal Diptera; small quantities of bottom mud were found in these guts. One exceptional fish had at least 5 larval cichlid fishes in its stomach, and further remains of small fishes in the intestine. Since this specimen is a female with spent ovaries, the larvae could be from its own brood (assuming, of course, that the species is a mouth-brooder).

The 8 specimens from a shallower locality (Murchison Bay, at a depth of 50 feet) had ingested considerable quantities of mud; in most cases this is the only material present, but in 2 fishes fragments of pupal Diptera were identified. Possibly the high proportion of mud in the guts is unnatural and due to the fishes being, as it were, force-fed whilst the trawl was dragged along and through the near-liquid mud.

Breeding. In the sample available, all fishes less than 80 mm. S.L. are immature (all these are females); 2 larger fishes (females 101 and 96 mm. S.L.) are also immature although other fishes of the same length are adult. The largest fishes are females.

There is a tendency for the right ovary in ripe females to be larger than the left one, but a definite asymmetry in ovarian development could not be detected.

Diagnosis and affinities. *Haplochromis dolichorhynchus* closely resembles *H. tridens* (see note on synonymy). When *H. tridens* was redescribed (Greenwood, 1967) the existence of *H. dolichorhynchus* was unknown, and the species appeared to be very distinctive. But, since that time trawling surveys in the deeper waters of Lake Victoria have produced a number of species which, together with *H. tridens* form a “*tridens*” complex of at least 5 species, and probably a sixth. Thus some

of the remarks made by Greenwood (*op. cit.*, pp. 97 and 99) about *H. tridens* (particularly with reference to the enlarged cephalic lateral line pores, the dentition, the general facies and the affinities of the species) are no longer valid.

Two species of the "*tridens*" complex are anatomically and superficially more distinct than the others, and need not be considered at this point (but see pp. 48 and 52). The more obviously similar species are *H. dolichorhynchus*, *H. tyrianthinus* (p. 40), *H. chlorochrous* (p. 44) and *H. tridens*.

As mentioned above, superficially *H. tridens* and *H. dolichorhynchus* resemble one another fairly closely. There is complete overlap in many morphometric characters, and the dentition is similar except that in *H. dolichorhynchus* the teeth are more slender and there are fewer tricuspid teeth in the outer row of either jaw.

The species also differ in the following characters: the body is slightly deeper in *H. tridens* (30.1–36.2, $M = 33.5\%$ of standard length, *cf.* 28.6–33.6, 31.9%); this is probably correlated with the more steeply sloping dorsal head profile in *H. tridens* (40°–45° *cf.* 20°–30°). The orbit in *H. tridens* is noticeably elliptical (longer than deep) but is virtually circular in *H. dolichorhynchus*. The snout in *H. dolichorhynchus* is slightly longer (30.3–37.7, $M = 34.2\%$ of head, *cf.* 28.0–34.8, $M = 30.4\%$ in *H. tridens*), a difference emphasised visibly by the beaked premaxilla of *H. dolichorhynchus* compared with the narrow medial part of that bone in *H. tridens*. Although the range of length/breadth ratios for the lower jaw shows complete interspecific overlap, there is a marked difference in the specific modes, with the jaw consistently narrower in *H. tridens* (mode 2.8 times as long as broad, *cf.* 2.1 times in *H. dolichorhynchus*). In *H. tridens* the posterior tip of the maxilla generally extends to a point below the eye (often to one below the pupil), but in *H. dolichorhynchus* it does not even extend to below the anterior margin of the orbit; the mouth in *H. tridens* is usually less oblique than in *H. dolichorhynchus* (horizontal to *ca.* 10°, *cf.* 10°–20°, mode *ca.* 20°).

Unfortunately the live coloration of *H. tridens* is unknown, but the two species clearly differ in preserved coloration (*cf.* p. 37 above with p. 99 in Greenwood, 1967). *Haplochromis tridens* has no bars or longitudinal bands in either sex but all female *H. dolichorhynchus* show a longitudinal band (sometimes interrupted, sometimes faint) and vertical bars are present in males. Another difference is the very dark ventral pigmentation of adult male *H. dolichorhynchus* compared with the light grey-silver of *H. tridens*.

Haplochromis dolichorhynchus closely resembles *H. tyrianthinus*, a resemblance which extends to similarities in the live coloration of males. The principal diagnostic characters lie in the dentition and the slope of the head, but there are other, although less clear-cut, differences.

The outer teeth in *H. tyrianthinus* are slender and fine, with unicuspid predominating. The cusp in these teeth is a little compressed, but the neck and body of the tooth are distinctly cylindrical in cross-section. In contrast the commonest tooth form in *H. dolichorhynchus* is the bicuspid; these teeth are slender but compressed both at the crown and in the body. Unicuspid teeth are rare in the outer tooth row of this species, and when present are more compressed than are the unicuspid teeth in *H. tyrianthinus*.

The dorsal head profile of *H. tyrianthinus* is more curved than in *H. dolichorhynchus*, and this feature, combined with a broader snout, gives *H. tyrianthinus* a more "heavy-headed" appearance than *H. dolichorhynchus*. Again, the distinctly beaked premaxilla of *H. dolichorhynchus* accentuates the impression of an elongate, sharp-pointed profile.

The orbit of *H. dolichorhynchus* is almost circular, that of *H. tyrianthinus* clearly longer than deep. The maxilla of *H. dolichorhynchus* does not reach the level of the anterior orbital margin, but in *H. tyrianthinus* it reaches that level or somewhat further posteriorly.

Although *H. dolichorhynchus* seems closely related to *H. chlorochrous*, superficially the two species are rather distinct. When alive they are immediately distinguishable: males of *H. dolichorhynchus* have a purple ground colour, those of *H. chlorochrous* a green one; females too are distinguishable on their coloration, being blueish-purple and lime-green in the species respectively.

Anatomically, the species may be separated by the broader snout of *H. chlorochrous* (0.9–1.0, mode 0.9 times as long as broad, cf. 1.0–1.4, mode 1.1 times), the more oblique lower jaw of *H. chlorochrous* and the less steeply inclined dorsal head profile of *H. dolichorhynchus*. The dentary of *H. chlorochrous* differs from that of *H. dolichorhynchus* in having the flare less pronounced and confined to the posterior and posterolateral parts of the bone (see p. 37 above). Finally, it may be noted that the neurocranium of *H. dolichorhynchus*, although essentially of the same type as that found in other species of the "*tridens*" group, differs in having the preorbital region somewhat more protracted.

The possible phyletic position of *H. dolichorhynchus* and other members of the "*tridens*" species complex will be discussed later (see p. 51).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.168 (Holotype)	Murchison Bay (30 feet) . . .	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.191–196	Buvuma Channel, W. of Nienda and Vuga isls. (108 feet) . . .	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.177–190	North of Nsadzi isl. (70–100 feet) .	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.169–176	Murchison Bay (30 feet) . . .	E.A.F.F.R.O.

Haplochromis tyrianthinus sp. nov.

(Text-figs. 25 and 26)

HOLOTYPE: an adult female 100.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.135) from north of Nsadzi island.

The trivial name (from the Greek) refers to the predominantly purple colours of male fishes.

DESCRIPTION: based on 15 fishes (including the holotype), 85.0–105.0 mm. S.L.

Depth of body 27.3–32.6 ($M = 30.6$) % of standard length, length of head 32.2–35.0 ($M = 33.7$) %.

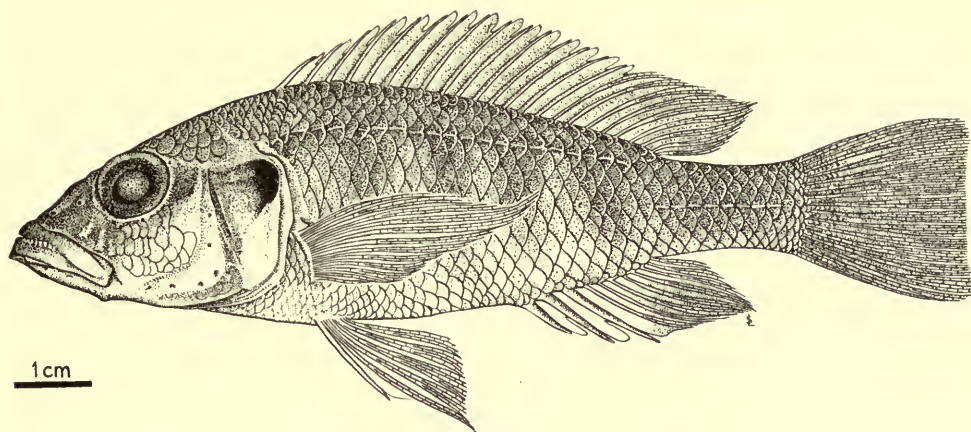


FIG. 25. *Haplochromis tyrianthinus*. Holotype. Drawn by Sharon Lesure.

Dorsal head profile slightly curved, sloping at an angle of 30° – 40° ; premaxillary pedicels moderately prominent. Lateral line tubes and pores of the preorbital bone prominent.

Preorbital depth 15.2–18.3 ($M = 17.1$) % of head, least interorbital width 15.2–18.3 ($M = 17.4$) %. Snout 0.9–1.0 (mode) times as long as broad, its length 29.3–35.2 ($M = 32.4$) % of head; snout length in this sample appears to show negative allometry with standard length. Orbit slightly elliptical (i.e. longer than deep), diameter of eye 26.1–29.3 ($M = 27.7$) % of head, depth of cheek 20.0–25.3 ($M = 22.9$) %.

Caudal peduncle 16.2–19.2 ($M = 18.1$) % of standard length, 1.4–1.9 (modal range 1.6–1.8) times as long as deep.

Mouth somewhat oblique, sloping at an angle of 15° – 20° (mode); a horizontal line drawn from the upper anterior tip of the lower jaw passes below the orbit or less commonly through the lowermost part of the eye. Jaws equal anteriorly (rare) or the lower projecting slightly; lower jaw with a distinct but not prominent mental protuberance, its length 44.3–52.8 ($M = 47.5$) % of head, and 1.7–2.2 (mode 2.0) times its breadth. Premaxilla somewhat expanded medially; posterior tip of maxilla reaching a vertical through the anterior orbital margin or to slightly beyond this point.

Gill rakers: 9 (mode) or 10 on the lower part of the first arch, the lower 1–3 rakers reduced, the upper 4 or 5 flattened with at least some anvil-shaped; the intervening rakers are of varied form (from short and stout to relatively long and slender) but none is flattened.

Scales: ctenoid; lateral line with 31 (f.2), 32 (f.2), 33 (f.8) or 34 (f.3) scales, cheek with 3 or 4 rows. Five to 6 (mode 5½) scales between the dorsal fin origin and the upper lateral line, 6–7 (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.11), 25 (f.3) or 26 (f.1) rays, comprising 14 (f.1), 15 (f.11) or 16 (f.3) spines and 8 (f.1), 9 (f.10) or 10 (f.4) branched rays. Anal with 11 (f.6) or 12 (f.9) rays comprising 3 spines and 8 or 9 branched rays. Pectorals 25.7–30.0

($M = 29.3$) % of standard length. Pelvics with the first ray produced in both sexes, but proportionately more so in adult males. Caudal truncate, scaled on its proximal half.

Teeth. The gently recurved *outer teeth* are slender, fine and nearly cylindrical in cross-section, but have slightly compressed crowns (Text-fig. 26). In the *upper jaw*, unicuspid, slenderly caniniform teeth predominate although slender bi- or weakly bicuspid teeth occasionally occur among the unicuspids in all parts of the row. The posterior outer teeth are sometimes tricuspid.

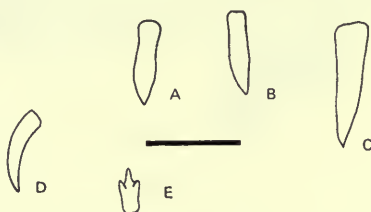


FIG. 26. *Haplochromis tyrianthinus*. A-D upper jaw teeth. A-C: in anterior view, D: in lateral view. Tooth C is from a larger individual than the other teeth. E: postero-lateral tooth from the dentary. Scale equals 1 mm.

In the lower jaw, the posterior teeth are generally tricuspid and slightly larger than their counterparts in the upper jaw. The posterolateral teeth can be an admixture of tri- and bicuspids, or bicuspids alone; a few fishes have unicuspids in this position. The other lower teeth in most individuals are slender unicuspids, but some bi- and weakly bicuspid teeth are sometimes found among the unicuspids.

There are 70-86 ($M = 74$) teeth in the outer row of the upper jaw.

Most of the *inner teeth* are tricuspid, but in some fishes the outermost row is composed of slender unicuspids; very occasionally all the inner teeth are unicuspid. The median cusp of inner tricuspids is noticeably elongate.

All inner teeth are obliquely implanted, some lying almost horizontally; there are 2 or 3 (mode) rows in the upper jaw, and 2 (rarely 1 or 3) rows in the lower jaw.

Osteology. The *neurocranium* of *H. tyrianthinus* closely resembles that of *H. dolichorhynchus* (see p. 36) but is slightly less protracted in the preorbital region.

The dentigerous surface of the *premaxilla* is moderately expanded anteromedially but it is not so distinctly beaked as the premaxilla of *H. dolichorhynchus*; the pedicels are shorter than the dentigerous arms.

The *dentary* is flared like that of *H. dolichorhynchus* (see p. 37), and the short mental protuberance is moderately pronounced.

The toothed surface of the *lower pharyngeal bone* is slightly broader than long or, occasionally, equilateral. The teeth are cuspidate, relatively fine and usually rather widely spaced in from 24-36 rows; in some fishes, however, the teeth are finer, and more regularly and closely arranged in 30-36 rows.

Coloration in life. Detailed live colour notes are not available for this species but it was noted (J.M.G.) that adult males have a bright and intense purple coloration on the dorsal and lateral aspects of the body.

Coloration of preserved material. Adult males are brownish, lightest on the chest where a faint silver overlay is visible; the branchiostegal membrane is faintly grey. Very faint traces of 5 or 6 vertical bars are visible on the flanks and caudal peduncle, those over the body intergrade with the generally darker brown colour of the belly and ventral body region above and posterior to the anal fin. A faint lachrymal stripe is visible, being most intense immediately below the eye.

Dorsal, caudal and anal fins are grey, the lappets of the dorsal black, as is the membrane between the anal spines; the central region of the caudal fin is darker than the upper and lower parts. The pelvic fins are black.

Females are light brown above, shading to beige ventrally, and with faint traces of a silvery overlay on the chest and belly in some specimens. Very faint traces of about 5 broad vertical bars are visible on the flanks and caudal peduncle; the bars do not reach the ventral profile. In some specimens there is a faint midlateral dark stripe, most intense over the posterior half of the body. Dorsal, caudal and anal fins are greyish, the pelvics hyaline.

Ecology. Habitat. The species is known from only one locality, north of Nsadzi island. Specimens were obtained from a trawl fished over a mud bottom at a depth of 70–100 feet.

Food. One of the 10 guts examined was empty, one contained fragments of a small cichlid fish in the stomach and further fish remains in the intestine; the other 8 all yielded fragmentary remains of Crustacea (probably *Caridina* sp.). In only 2 guts was there any bottom detritus.

Breeding. Only one specimen (a female 85 mm. S.L.) is a juvenile; the smallest male (99 mm. S.L.) shows an advanced state of testicular development. There is no clear-cut indication of asymmetrical ovarian development.

Diagnosis and affinities. Within the “*tridens*” species complex, *H. tyrianthinus* most closely resembles *H. chlorochrous* and *H. dolichorhynchus*. Characters distinguishing *H. tyrianthinus* from the latter species (which it also resembles in live coloration) are discussed on p. 39. Live specimens (of either sex) are immediately distinguished from *H. chlorochrous* by their coloration which is basically purple to blue in *H. tyrianthinus* and green in *H. chlorochrous*.

Anatomically, *H. tyrianthinus* is distinguished from *H. chlorochrous* principally by dental characters and differences in head shape. The outer row of teeth in *H. tyrianthinus* is composed, mainly, of slender unicuspid, circular in cross-section over most of their length except for a slight compression of the crown. In *H. chlorochrous*, on the other hand, there is a mixture of bi- and unicuspid in this row, and the teeth although slender are relatively compressed, especially at the crown. There is also a difference in the pharyngeal teeth of the two species, but this character shows a greater degree of overlap than does the difference in jaw teeth. In most specimens of *H. tyrianthinus* the lower pharyngeal teeth are coarser, fewer and more widely spaced (particularly in the posterolateral corners of the dentigerous area) than are the teeth in *H. chlorochrous*. Small individuals of *H. tyrianthinus*, however, have a lower pharyngeal dentition like that of adult *H. chlorochrous*.

The lower jaw of *H. tyrianthinus* slopes less steeply than in *H. chlorochrous* (15° – 25° , mode 20° , cf. 20° – 35° , mode 30°); as a result, a horizontal drawn from the upper

tip of the lower jaw passes below the orbit (or through the lower orbital margin) in *H. tyrianthinus* but through the lower or middle part of the eye in *H. chlorochrous*.

The snout in *H. tyrianthinus* is somewhat narrower than in *H. chlorochrous* (0.9–1.0, mode 1.0, times as long as broad, cf. 0.9–1.0, mode 0.9, times in *H. chlorochrous*) and the dorsal head profile is gently curved, both factors contributing to the distinctly different physiognomy of the two species.

Osteologically, the principal interspecific differences lie in the more antero-posteriorly extensive and deeper flare of the outer face of the dentary in *H. tyrianthinus*.

Haplochromis tyrianthinus also resembles *H. tridens*, but is distinguished by its preserved coloration (especially the presence of vertical bars on the flanks) more oblique mouth, broader lower jaw (model length/breadth ratio 2.0 cf. 2.8 in *H. tridens*), less steeply declined and more curved upper head profile (30°–40°, cf. 40°–45° in *H. tridens*), and by its slender, predominantly unicuspid outer teeth.

The possible phyletic relationships of *H. tyrianthinus* are discussed on p. 51.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.135 (Holotype)	North of Nsadzi isl. (70–100 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.136–149	North of Nsadzi isl. (70–100 feet)	E.A.F.F.R.O.

Haplochromis chlorochrous sp. nov.

(Text-figs. 27–29)

HOLOTYPE: an adult male 102.5 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.310) from water 70–100 feet deep between Nsadzi island and the mainland.

The trivial name (from the Greek) refers to the distinctive green colour of adult fishes.

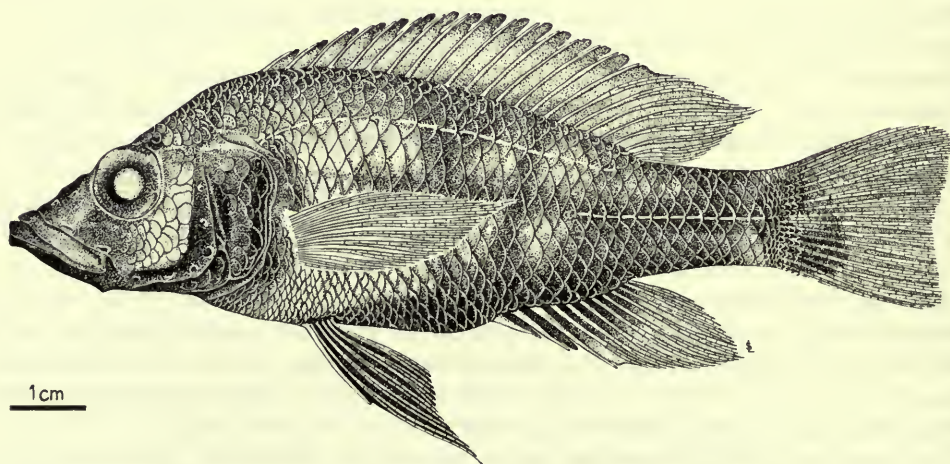


FIG. 27. *Haplochromis chlorochrous*. Holotype. Drawn by Sharon Lesure.

DESCRIPTION: based on 19 specimens (including the holotype), 70.0–120.0 mm. S.L.

Depth of body 29.5–34.5 ($M = 32.0$) % of standard length, length of head 32.0–35.4 ($M = 34.0$) %. Dorsal head profile straight or very slightly concave, sloping at an angle of 30°–40°; premaxillary pedicels only just apparent beneath the skin of the snout. Cephalic lateral line pores are prominent.

Preorbital depth 15.6–19.4 ($M = 17.3$) % of head, least interorbital width 15.6–20.2 ($M = 17.7$) %. Snout 0.9–1.0, mode 0.9 times as long as broad, its length 29.5–35.0 ($M = 32.3$) % of head. Orbit slightly elliptical (i.e. longer than deep), diameter of eye 25.4–29.0 ($M = 18.2$) % of head, depth of cheek 20.0–25.0 ($M = 22.6$) %.

Caudal peduncle 15.4–20.3 ($M = 18.2$) % of standard length, 1.3–1.9 (modal range 1.5–1.6) times as long as deep.

Mouth somewhat oblique (*ca.* 20°–35°, mode 30°); a horizontal line drawn from the upper tip of the lower jaw passes through the lower quarter of the eye or even through the centre of the eye. Lower jaw projecting, its length 44.3–51.8 ($M = 47.0$) % of head, 1.6–2.1 (mode 1.9) times as long as broad; mental protuberance moderate. Premaxilla moderately expanded anteromedially. Posterior tip of the maxilla reaching a vertical through the anterior orbital margin or a little more posteriorly to below the eye.

Gill rakers: Nine or 10 (rarely 8), on the lower part of the first arch. The lower 1–4 rakers are reduced, the upper 3 or 4 flattened, sometimes lobed; intervening rakers are relatively short and stout.

Scales: ctenoid; lateral line with 31 (f.1), 32 (f.7), 33 (f.9) or 34 (f.1) scales, cheek with 3 or 4, rarely 5, rows. Five and a half to 6½ (mode 6) scales between the dorsal fin origin and the upper lateral line, 6–7 (mode), rarely 5, between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.17) or 25 (f.2) rays, comprising 14 (f.1), 15 (f.17), or 16 (f.1) spines and 9 (f.17) or 10 (f.2) branched rays. Anal with 11 (f.6) or 12 (f.13) rays, comprising 3 spines and 8 or 9 rays. Pectoral 26.8–30.4 ($M = 28.7$) % of standard length. Pelvic fins with the first ray produced, not apparently showing any length correlation with sex, except that it is relatively longer in adults than in juveniles. Caudal truncate, scaled on its proximal half.

Teeth. In the *outer* tooth row of the *upper jaw* there is an admixture of slender unicuspid and slender, unequally bicuspid teeth, both types having relatively compressed crowns (Text-fig. 28); the bicuspid teeth may be so weakly cuspidate as to appear unicuspid. In the smallest fish (70 mm. S.L.) some tricuspid teeth are

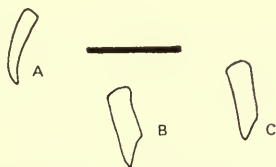


FIG. 28. *Haplochromis chlorochrous*. A–C upper jaw teeth. A: in lateral view. B and C: in anterior view. Scale equals 2 mm.

interspersed among the bicuspid. Posteriorly and posterolaterally the teeth are usually small and tricuspid, but in some specimens unicuspid or bicuspid are present in this position.

There are 66–86 ($M = 74$) teeth in the outer row of the upper jaw.

Generally, the *outer teeth* in the *lower jaw* are similar to those in the upper jaw, but in a few fishes all except the posterior teeth are slender bicuspid. The posterior teeth are usually tricuspid and slightly larger than their counterparts in the upper jaw.

All teeth in the *inner rows* are tricuspid, and implanted somewhat obliquely. There are 2 or 3 (mode), rarely 4, rows in the upper jaw and 2 (mode) or 3, rarely a single row, in the lower jaw.

Osteology. The neurocranium of *H. chlorochrous* is indistinguishable from that of *H. tyrianthinus*, and premaxillary shape in the two species is also identical. The *dentary*, however, differs in that the flared region is restricted to a more posterior position (see p. 42). Consequently the anterior and anterolateral face of each ramus is almost flat, only the posterior and posterolateral faces showing any concavity. The mental protuberance is stout but not especially prominent.

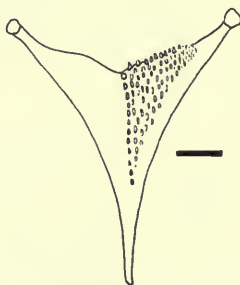


FIG. 29. *Haplochromis chlorochrous*. Lower pharyngeal bone. Scale equals 2 mm.

The dentigerous surface of the *lower pharyngeal bone* (Text-fig. 29) is as long as broad, or very slightly broader. The teeth are fine, cuspidate, and closely arranged in 30–36 regular rows.

Coloration in life. *Adult males* are dark green on the dorsal surfaces of the body and head, lighter green on the flanks which are crossed by 5 faint, dark, vertical bars; the ventral body surfaces are black.

Dorsal fin is greenish-yellow basally, hyaline distally, with faint traces of orange-red maculae. The caudal and pectoral fins greenish basally, hyaline distally. The anal is black basally, almost hyaline distally, the 2 or 3 ocelli are orange. Pelvic fins are black.

Females have the dorsal body surfaces lime-green, the flanks bright yellow, and the ventral body surfaces silver. There is a faint midlateral longitudinal stripe, and the flanks are crossed by 4 or 5 vertical bars. The head and upper lip are green, the lower lip yellow. All fins are yellowish-green.

Preserved coloration. *Adult males* have a yellow-brown ground coloration, the snout greyish, the lower jaw, ventral part of the preopercular region and the lower half of the operculum black. A broad and diffuse lachrymal stripe is usually visible.

The lower half of the body posterior to the vent is black or very dark brown; a narrow tongue of this dark area extends forward onto the ventral aspect of the belly as far as the base of the pelvic fins. Three to 5 dark vertical bars cross the posterior flanks; ventrally the bars merge with the black lower aspects of the body. A very faint, often incomplete, dark midlateral stripe is generally visible, extending forward from the dark posterior region almost to the opercular margin.

Dorsal fin dark grey, lappets and margin of the soft part black. The caudal fin is dark grey, indistinctly blotched with black near the base in some specimens, weakly maculate in others. Anal fin is black basally and between the spines, dark grey distally. The pelvic fins are black.

The single immature male is uniformly yellow-brown except for a darker snout region, faint lachrymal stripe, dusky lower jaw and preopercular region. The dorsal fin is grey with black lappets and margin to the soft part, the caudal and anal fins greyish, the anal dusky between the spines; the pelvics are dusky, becoming black over the anterior third.

Females have a light brown ground colour, darker dorsally and on the snout which is greyish in some individuals. A faint, narrow and interrupted dark midlateral stripe runs from behind the opercular margin to the base of the caudal fin where it is slightly expanded. The dorsal fin is greyish, the lappets black and the soft part entirely or partly maculate. Caudal fin grey, and indistinctly maculate. Anal hyaline, greyish along its margin in adults. Pelvic fins hyaline, but often greyish over the anterior third to half in adults.

Ecology. Habitat. All the specimens examined came from trawl hauls over a mud substrate, and at a depth of 70 to 100 feet, in the area between Nsadzi island and the mainland. One of us (J.M.G.) has recorded the species in several other localities, viz: south of Nsadzi island (130–160 feet, over mud), near Bulago island (55–75 feet, over mud), between the south side of Buvuma island and the northern shore of Bugaia island (105 feet, over mud) and between Mwama and Bugaia islands (200 feet, over mud).

Food. Two of the 15 guts examined were empty. Of the remainder, 2 contained only mud, and 11 mud with fragments of Crustacea (probably *Caridina* sp.).

Breeding. Three males (77, 78 and 89 mm. S.L.) are immature, as are 3 females (70, 72 and 74 mm. S.L.); all the larger fishes are adults. In the 7 adult females examined there is a distinct tendency for the right ovary to be larger than the left, irrespective of the individual's sexual state.

Diagnosis and affinities. *Haplochromis chlorochrous* is compared with *H. dolichorhynchus* on p. 40, and with *H. tyrianthinus* on p. 43; in life its green coloration serves as an immediate diagnostic character.

From *H. tridens*, the fourth member of this species complex, *H. chlorochrous* is distinguished principally by its more oblique and broader lower jaw (angle of mouth 20°–35°, mode 30°, cf. horizontal to 10° in *H. tridens*; lower jaw 1.6–2.1, mode 1.9 times as long as broad, cf. 2.0–2.8, mode 2.8 times in *H. tridens*), and by the presence of vertical bars on the flanks of preserved adult males (a longitudinal stripe in females) as well as by the very dark ventral coloration on the posterior part of the body in males.

The possible phyletic relationships of *H. chlorochrous* are discussed on p. 51.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.310 (Holotype)	Between Nsadzi isl. and mainland (70-100 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.311-328	Between Nsadzi isl. and mainland (70-100 feet)	E.A.F.F.R.O.

Haplochromis cryptogramma sp. nov.

(Text-figs. 30 and 31)

HOLOTYPE: an adult male 86.5 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.197) from the Bulago-Tavu bank at a depth of 50-75 feet.

The trivial name refers to the fancied resemblance of the midlateral longitudinal stripes to symbols in the Morse code.

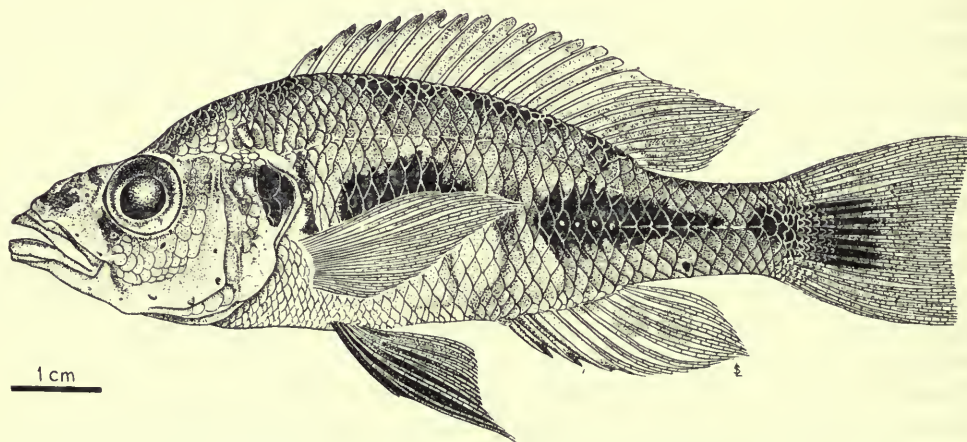


FIG. 30. *Haplochromis cryptogramma*. Holotype. Drawn by Sharon Lesure.

DESCRIPTION: based on 23 specimens (including the holotype) 55.0-94.0 mm. S.L. Depth of body 30.2-35.8 ($M = 33.6$) % of standard length, length of head 34.5-38.8 ($M = 35.7$) %.

Dorsal head profile sloping at an angle of 35°-40°, noticeably concave, the prominent premaxillary pedicels tending to exaggerate the concavity and giving the profile a characteristic outline (Text-fig. 30).

Preorbital depth 14.3-17.7 ($M = 15.4$) % of head, least interorbital width 20.3-23.9 ($M = 22.0$) %. Snout prominent in lateral view, 1.0-1.5 (mode 1.2) times as long as broad, its length 28.6-35.5 ($M = 32.7$) % of head; eye diameter 25.8-31.6 ($M = 28.7$) %, the orbit almost circular; depth of cheek 15.8-21.5 ($M = 19.0$) %.

Caudal peduncle 17.5–22.7 ($M = 19.2$) % of standard length, 1.5–2.0 (modal range 1.8–1.9) times as long as deep.

Mouth slightly oblique, sloping at an angle of 10° – 15° . Jaws equal anteriorly or, less commonly, the lower projecting; premaxilla slightly expanded anteromedially. Lower jaw 40.0–48.5 ($M = 44.8$) % of head, 2.0–2.7 (modal range 2.3–2.5) times as long as broad; mental protuberance slight. Posterior tip of the maxilla generally reaching a vertical through the anterior part of the orbit, but only to the anterior orbital margin in a few specimens.

Gill rakers: Eight or 9 (rarely 7 or 10) on the lower part of the first arch, the lower 2 or 3 rakers reduced, the remainder of varied form, from short and stout through slender to flattened with some of the upper rakers anvil-shaped.

Scales: ctenoid; lateral line with 31 (f.2), 32 (f.7) or 33 (f.8) scales (several specimens have lost their scales, hence these figures are derived from only 17 fishes); cheek with 3 rows (rarely 2 or 4). Five to $6\frac{1}{2}$ (mode $5\frac{1}{2}$) scales between the upper lateral line and the dorsal fin origin, 6–7 (mode 7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.5), 24 (f.17) or 25 (f.1) rays, comprising 15 (f.16) or 16 (f.7) spines and 8 (f.11) or 9 (f.12) branched rays. Anal with 10 (f.1), 11 (f.21) or 12 (f.1) rays, comprising 3 spines and 7–9 branched rays. Pectoral 25.0–32.0 ($M = 28.3$) % of standard length. Pelvic fin with the first ray somewhat produced in both sexes, probable a little more so in adult males. Caudal truncate or slightly emarginate, scaled on its proximal half.

Teeth. The *outer row* of teeth in the *upper jaw* (except posteriorly) is composed mainly of unequally bicuspid, relatively stout teeth; however, most fishes have some tricuspid teeth interspersed amongst the bicuspids both anteriorly and laterally (Text-fig. 31). A few exceptional individuals have a predominance of tricuspid teeth in this row. Posteriorly and posterolaterally in this jaw there are either unicuspid and bicuspid teeth, or tricuspids alone; rarely, all three types of teeth occur in this position.

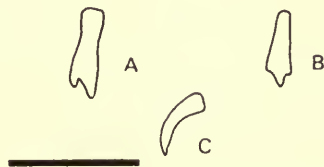


FIG. 31. *Haplochromis cryptogramma*. A–C upper jaw teeth. A and B: teeth from anterior part of outer row, in anterior view. C: tooth A in lateral view. Scale equals 2 mm.

There are 50–78 ($M = 68$) teeth in the outer row of the upper jaw.

In the *lower jaw*, the teeth are similar to those in the upper jaw except that there are fewer tricuspids anteriorly and anterolaterally. Posteriorly and posterolaterally most fishes have tricuspid teeth, but in a few individuals the teeth in this position are bicuspid, or there is mixture of bi- and tricuspid teeth in this position.

The *inner series* is composed of obliquely implanted tricuspid teeth arranged in 2 or 3 rows in the upper jaw, and 1 or 2 rows in the lower jaw.

Osteology. The *neurocranium* of *H. cryptogramma* is essentially of the type found in the "*tridens*" species complex (*H. tridens*, *H. dolichorhynchus*, *H. tyrianthinus* and *H. chlorochrous*). It differs, however, in having a somewhat broader interorbital region and a lower supraoccipital crest.

The *premaxilla* is noticeably expanded medially and anteromedially, to give it a beaked appearance. The pedicels are longer than the dentigerous arms.

The *dentary* resembles that of *H. dolichorhynchus* because the lateral face is strongly flared and the resulting concavity extends forward almost to the symphyseal region. The lateral line system in the dentary shows no signs of hypertrophy.

The dentigerous surface of the *lower pharyngeal bone* is as broad as long or slightly broader than long. The teeth are relatively fine with, in some fishes, those of the median rows slightly coarser. A striking feature is the regularity with which the teeth are arranged in 26-30 rows.

Coloration in life. *Adult males* have the dorsal aspect of the head and body blueish-grey, shading to yellowish on the flanks, and silver ventrally. A reddish flush is usually present on the opercular and pectoral regions, and is most intense in ripe males. Two black bars cross the snout, and another, fainter, bar crosses the nuchal region behind the eyes. On the body there are 2 (but sometimes fused) black blotches at the dorsal fin base, and one on the dorsal part of the caudal peduncle. Midlaterally there is a prominent dark band interrupted in at least 2, often 3, places to give a series of short and long lines. The posterior line extends well onto the caudal fin. The dorsal fin is hyaline, with black lappets. The caudal fin is either colourless or, in ripe individuals, with a red flush. The anal is colourless or whiteish (especially in sexually active fishes) and has 2 or 3 yellow ocelli. The pelvic fins are uniformly black.

Females have a body coloration like that of males but are without the red flush; the cephalic and flank markings are present as in males, but the nuchal bar is usually less distinct. The caudal and anal fins are yellow, the other fins hyaline.

Coloration in preserved material. In *both sexes* the ground coloration is silvery white. A series of broad but elongate black blotches runs midlaterally along the flanks and caudal peduncle. The anterior (and shortest) blotch lies on the operculum, the posterior streak extends onto the caudal fin and may even reach to near the posterior border. A series of elongate blotches (sometimes confluent into 2 or even a single smudge) lies below the dorsal fin origin. In some fishes there are faint traces of 3 or 4 vertical bars on the flanks. The snout is crossed by 2 transverse bands and a faint nuchal bar is generally visible.

In *males* the dorsal fin is greyish, with black lappets, and a faintly sooty margin to the soft part; the anal is also greyish with black lappets, and faint off-white ocelli. The caudal is greyish to hyaline, somewhat darker basally and with an intense black blotch extending over at least the anterior half.

Females have all the fins hyaline but with a faint duskiness along the margin of the dorsal fin.

Ecology. Habitat. The species is known from 2 areas, namely, Namone point (at a depth of *ca.* 30 feet) and in the region of the Bulago-Tavu bank at a depth of 50-75 feet. In both areas the substrate is mud.

Food. The gut contents of 20 specimens (from one locality, near the Bulago-Tavu bank) were examined; of these, 4 were empty. The remainder all contained either pupal Diptera or adult Crustacea (especially *Caridina* sp.); less commonly, both types of food were present. In 8 guts, small quantities of bottom mud were also recorded.

Breeding. All the specimens examined (55–94 mm. S.L.) are adult. The right ovary is larger than the left in 6 of the 10 females available.

Diagnosis and affinities. The dentition and syncranial architecture of *H. cryptogramma* suggest close affinity with the “*tridens*” species complex (see p. 52). At the species level, however, *H. cryptogramma* is immediately distinguished from all other members of the group by the highly distinctive colour patterns in both live and preserved specimens.

Haplochromis cryptogramma is also distinguishable from other members of the “*tridens*” complex by its broader interorbital region.

Despite these differences we would include *H. cryptogramma* as a member of the “*tridens*” species group. Its phyletic position will, therefore, be discussed in relation to the rest of the group.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.197 (Holotype)	Bulago-Tuva bank (50–75 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.198–214	Bulago-Tavu bank (50–75 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.215–219	Namone Point (Hannington Bay) (ca. 30 feet)	E.A.F.F.R.O.

The affinities of the *H. tridens* species group

The discovery of *H. dolichorhynchus*, *H. tyrianthinus*, *H. chlorochrous* and *H. cryptogramma* considerably modifies Greenwood's (1967) remarks about the affinities of *H. tridens*. That species was thought to occupy an isolated position among the Lake Victoria species flock, but the new species show that there is, in fact, a group of at least 5 “*tridens*”-like species.

All are characterized by their dentition, general facies and syncranial architecture (see above in the relevant sections of the species' descriptions). Although these various characters provide a means of delimiting the group as a whole, there still remains the problem of its relationships with other species complexes.

The unusual dental characteristic of the “*tridens*” group lies in the high proportion of tricuspid teeth in the outer tooth row of both jaws. The morphology of the non-tricuspid teeth is not outstanding; similar teeth occur in many other species-groups (except, of course, the most generalized) and are common types in the “*prognathus*” complex of piscivorous species (see Greenwood, 1967, p. 109).

The body-form in the “*tridens*” complex also occurs in the “*prognathus*” group, as does their type of syncranial morphology and organization. Indeed, the neurocranium of *H. dolichorhynchus* is very like that of *H. prognathus* itself, and the neurocranium in other group members does not depart greatly from this type.

These various similarities suggest to us that the "*tridens*" species complex is derived from the same stem as the "*prognathus*" group, and probably from an ancestor resembling the present-day *H. prognathus*.

The 4 species described in this paper, together with *H. tridens*, form a close-knit complex in which *H. cryptogramma* is the most deviant member, at least in its superficial appearance. But, if *H. arcanus* (see p. 54) is to be included in the "*tridens*" complex, it would qualify for that position. For the moment, however, we would prefer to leave open the question of the affinities of *H. arcanus*.

***Haplochromis arcanus* sp. nov.**

(Text-fig. 32)

HOLOTYPE: an adult male 127.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.19) from south of Nsadzi island, at a depth of between 130–160 feet.

The trivial name (from the Latin for secret) refers to our uncertainty about the relationships of this species within the Lake Victoria *Haplochromis* species-flock.

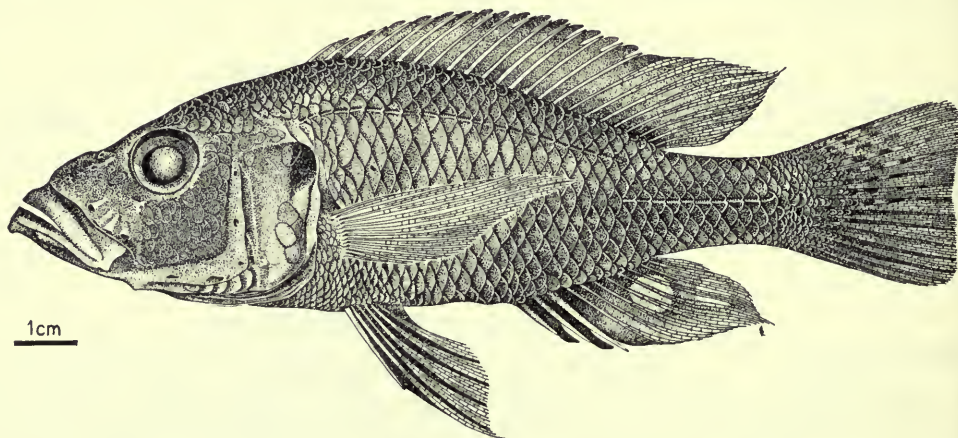


FIG. 32. *Haplochromis arcanus*. Holotype. Drawn by Sharon Lesure.

DESCRIPTION: based on 9 specimens (including the holotype) 104.0–142.0 mm. S.L. Depth of Body 30.8–33.3 ($M = 31.9$) % of standard length, length of head 37.3–39.4 ($M = 38.1$) %.

Dorsal head profile almost straight (but with a slight supraorbital depression which is intensified by the prominent premaxillary pedicels), sloping at an angle of 30°–35°.

Preorbital depth 17.3–19.8 ($M = 18.8$) % of head, least interorbital width 16.6–19.2 ($M = 18.1$) %. Snout 1.1–1.4 (mode 1.2) times as long as broad, its length 33.8–38.5 ($M = 35.7$) % of head, eye diameter 22.7–25.0 ($M = 24.1$), depth of cheek 22.2–26.0 ($M = 23.8$) %.

Caudal peduncle 13.7–18.3 ($M = 16.0$) % of standard length, 1.3–1.7 (mode 1.5) times as long as deep.

Mouth moderately oblique, sloping at an angle of 30°–35°; lower jaw with a distinct mental protuberance, projecting slightly, its length 47.0–51.8 ($M = 49.3$) %

of head, 1.9–2.2 (mode 2.1) times as long as broad. Premaxilla somewhat expanded anteromedially and thus slightly beaked. Posterior tip of the maxilla reaching a vertical slightly anterior to the orbital margin, or one reaching the orbit.

Gill rakers: 9–11 (mode 10) on the anterior part of the first gill arch, the lower 1–3 rakers reduced, the upper 3 or 4 flattened, expanded and often anvil-shaped; the intervening rakers are relatively stout.

Scales: ctenoid; lateral line with 31 (f.1), 32 (f.5), 33 (f.1) or 34 (f.2) scales, cheek with 4 (mode) or 5 rows. Six to 7 (mode 6) scales between the upper lateral line and the dorsal fin origin, 7–8 (mode), rarely 6, between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.5) or 25 (f.4) rays, comprising 14 (f.1), 15 (f.7) or 16 (f.1) spines and 9 (f.5) or 10 (f.4) branched rays. Anal with 11 (f.4), 12 (f.3) or 13 (f.2) rays, comprising 3 spines and 8–10 branched rays. Pectoral fin 26.2–31.7 ($M = 30.0$) % of standard length. Pelvics with the first ray produced. Caudal truncate, scaled on its basal half.

Teeth. Except in the smallest specimen (104 mm. S.L.), the *outer teeth* in *both jaws* are slender and unicuspid, those situated anteriorly and laterally in both jaws slightly recurved, but the posterolateral and posterior upper teeth strongly incurved.

The smallest fish has an admixture of weakly bicuspid and unicuspid teeth, and the posterolateral upper teeth are not strongly incurved.

There are 50–74 ($M = 64$) outer teeth in the upper jaw.

The *inner teeth* in most specimens are all tricuspid, but in a few individuals there is an admixture of uni- and bicuspid, with unicuspid predominating in the lower jaw. There are 2 or 3 rows of inner teeth in the upper jaw, and 2 rows in the lower jaw, all implanted at a slight angle.

Osteology. No complete skeleton of *H. arcanus* is available.

The *lower pharyngeal bone* has a triangular dentigerous surface which is as broad as, or slightly broader than, long. The teeth are fine, compressed and cuspidate, and are arranged in 26–30 rows. In some fishes the posterior teeth in the 2 median rows are noticeably coarser than their anterior congeners.

Coloration. The colours of live fishes are unknown.

Preserved material. *Males (adult)* have dark, yellowish-brown ground coloration with a faint duskiess on the chest and belly. The dorsal head surface and the snout are dusky, the branchiostegal membrane dusky in the opercular region but dark brown anteriorly. The dorsal fin is dusky, but with a darker basal region and black lappets. The caudal fin is very dark grey (almost black basally) with black maculae over most of its surface, the spots most concentrated on the upper half. Anal fin dark grey, dusky along its base and over the spinous part; ocelli large, lighter grey than the fin membrane but with a dark ring surrounding each ocellus. The pelvic fins are black.

Females (adult) have a greyish-yellow ground coloration dorsally, shading to light yellow-brown on the chest and belly; the snout and dorsal head surfaces dark grey. The dorsal fin is greyish with black lappets. Caudal fin greyish (darkest basally) with some dark maculae on the upper half. Anal hyaline or hyaline with a dark band

basally and another slightly below the distal margin. Pelvic fins hyaline or with a faint dusky marbling.

Ecology. Habitat. The species is known from only 2 localities; one, south of Nsadzi island at a depth of 130–160 feet over a mud bottom, the other north of Nsadzi island, also over a mud bottom but at a depth of 70–100 feet.

Food. No information is available; the guts examined were empty, and several specimens had been eviscerated before preservation.

Breeding. All 9 specimens are adult.

Diagnosis and affinities. At present we can say little about the affinities of *H. arcanus*. Superficially, the species resembles certain members of the “*tridens*” complex, particularly *H. tyrianthinus* and *H. dolichorhynchus*. However, it differs from all members of the “*tridens*” group in being without any tricuspid teeth in the outer tooth row of either jaw, and in having the posterolateral upper teeth strongly incurved.

Haplochromis arcanus also differs from *H. tyrianthinus* in head shape (especially the prominent premaxillary pedicels), its longer head (37.3–39.4, $M = 38.1\%$ S.L., cf. 32.2–35.0, $M = 33.7\%$), narrower snout (1.1–1.4, mode 1.2 times as long as broad, cf. 0.9–1.0, mode 1.0 times) and in having fewer and stouter teeth (this in addition to the dental differences noted above).

From *H. dolichorhynchus*, *Haplochromis arcanus* differs in having a slightly longer head, a markedly different profile (including a more oblique lower jaw) and in various dental details (especially the unicuspid and recurved outer teeth, the relatively stouter form of all outer teeth and their greater spacing).

The dentition of *H. arcanus* resembles that of *H. argenteus*, and there is a fairly close similarity in general facies, especially when specimens of comparable size are examined (see Greenwood, 1967, p. 84). *Haplochromis arcanus* differs from *H. argenteus* in having a larger eye (22.7–25.0, $M = 24.1\%$ of head, cf. 19.4–23.5, $M = 21.5\%$), broader lower jaw (1.9–2.2, mode 2.1 times as long as broad, cf. 2.3–3.1, modal range 2.8–3.0 times in *H. argenteus*), a longer pectoral fin (26.2–31.7, $M = 30.0\%$ S.L., cf. 24.1–29.7, $M = 25.0\%$), and smaller chest and nape scales (see Greenwood, *op. cit.*).

On the characters we have been able to study (and these exclude osteological ones), *H. arcanus* could be related to either the *H. tridens* species complex, or to *H. argenteus*. Since both the “*tridens*” group and *H. argenteus* are probably derived from an *H. prognathus*-like ancestor (see above, p. 51, and Greenwood, *op. cit.*) these bilateral affinities of *H. arcanus* would not be unexpected if it too is descended from a similar stem.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.19 (Holotype)	S. of Nsadzi isl. (130–160 feet) . . .	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.22–27	S. of Nsadzi isl. (130–160 feet) . . .	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.20–21	N. of Nsadzi isl. (70–100 feet) . . .	E.A.F.F.R.O.

Haplochromis decticostoma sp. nov.

HOLOTYPE: an adult male 199.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.292) from south of Nsadzi island, at a depth of 180 feet.

The trivial name (from the Greek *dektikos*: able to bite, and *stoma*: mouth) refers to the large mouth.

DESCRIPTION: based on 22 specimens (including the holotype), 129.0–229.0 mm. S.L.

Depth of body 32.9–40.1 ($M = 36.6$) % of standard length, length of head 36.1–42.0 ($M = 38.9$) %.

Dorsal head profile straight, sloping at an angle of 30°–35°, usually interrupted by the premaxillary pedicels. Pores of the cephalic lateral line system are fairly prominent, especially those on the preorbital which has a swollen appearance.

Preorbital depth 19.4–23.8 ($M = 21.7$) % of head length, least interorbital width 20.0–23.1 ($M = 21.6$) %. Snout 1.0–1.2 (mode 1.1) times as long as broad, its length 37.1–41.0 ($M = 38.9$) % of head. Eye diameter 17.9–22.6 ($M = 20.1$) % of head, eye/preorbital ratio 0.8–1.0 (mode 0.9); depth of cheek 26.4–31.3 ($M = 29.1$) %.

Caudal peduncle 14.4–18.7 ($M = 16.4$) % of standard length, 1.2–1.7 (mode 1.4) times as long as deep.

Mouth oblique, sloping at an angle of 30°–40°, lower jaw projecting slightly to strongly, its length 50.7–55.7 ($M = 53.0$) % of head, 1.6–2.3 (modal range 1.9–2.0) times as long as broad. A very prominent mental protuberance is developed, apparently a little longer in males than in females (but this point requires further checking on more specimens). Posterior tip of the maxilla reaching a vertical through a point slightly nearer the orbit than the nostril, or less frequently, somewhat more posteriorly, but never reaching a vertical through the anterior orbital margin.

Gill rakers: Nine or 10 (mode) on the lower part of the first gill arch, the lower 1–3 rakers reduced, the remainder short and stout, or relatively stout.

Scales: ctenoid; lateral line with 32 (f.9) or 33 (f.12) scales, cheek with 5 or 6 (mode 5) rows. Six and a half to 8 (mode 7½) scales between the upper lateral line and the dorsal fin origin, 6 (rarely) to 8 (mode) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.9) or 25 (f.10) rays, comprising 14 (f.1), 15 (f.16), or 16 (f.3) spines and 9 (f.13) or 10 (f.7) branched rays. Anal with 11 (f.1), 12 (f.16) or 13 (f.3) rays, comprising 3 spines and 8–10 branched rays. Pectoral 27.4–34.8 ($M = 29.7$) % of standard length. Caudal fin truncate, scaled on its proximal half. Pelvics with the first ray produced, proportionately more so in males than in females.

Teeth. The *outer teeth* in *both jaws* are unicuspid, long, and relatively curved, especially over the distal half. There are 56–80 ($M = 68$) teeth in the outer row of the upper jaw.

The inner teeth are also unicuspid and curved, and are implanted obliquely, especially in the upper jaw where they lie almost horizontally. The inner teeth are arranged rather irregularly in 3 or 4 rows in the upper jaw and in 2 or 3 rows in the lower jaw.

Osteology. The syncranium of *H. decticostoma* is very similar to that of *H. speikii* in most details. One possible interspecific difference in the neurocranium, the height and basal extent of the supraoccipital crest, cannot be substantiated without more osteological material of both species. Another probable difference is the more gently sloping preorbital profile in the skull of *H. decticostoma*.

The lower pharyngeal bone has a triangular dentigerous surface, as long as broad or somewhat broader (1.1–1.2 times). The lower pharyngeal teeth are fine, compressed and cuspidate, and are arranged in 24–28 irregular rows; teeth in the 2 median series are generally coarser than their lateral congeners.

Coloration in life. Males have a dark golden-brown ground coloration, the dorsal surfaces darkest and with iridescent blue highlights, shading to silver ventrally; an iridescent greenish to yellowish sheen extends over the flanks, opercular region and the cheeks.

Dorsal fin hyaline, darker (almost grey) proximally, lappets dark, soft part with orange-red streaks and spots. Anal hyaline but with a maroon flush distally, and with several orange ocelli (sometimes arranged in 2 rows). Caudal dark proximally, hyaline distally, with orange or red streaks and spots between the rays. Pelvic fins dusky.

Females. Except for the hyaline fins and absence of anal ocelli, the live coloration of females is like that of males.

Preserved material. Males have a brownish-grey coloration dorsally, becoming silver-grey on the ventral surfaces. The snout and preorbital region are dark grey, as are the lips and tip of the lower jaw (the latter almost black in some specimens). The cheek and opercular region are yellowish, the branchiostegal membrane yellowish to dead-white. In some specimens there is a very faint, narrow, but dark midlateral stripe separating the darker dorsal coloration from the lighter ventral tones; a very faint lachrymal stripe is visible in some fishes, being most intense near the angle of the jaws.

Dorsal fin greyish with dark lappets. Anal greyish basally, becoming hyaline distally, the numerous ocelli large and dead-white but sometimes with a faint grey overlay. Caudal greyish, with darker maculae. Pelvic fins dusky to black, the colour most intense on the anterior half of the fin.

Females are light yellowish-brown above, shading to yellowish-white on the chest and belly. The snout, upper lip and tip of the lower jaw are dusky grey, the cheek and opercular region yellowish. A faint dark spot situated behind the angle of the jaw seems to be comparable with the more intense part of the lachrymal stripe in males.

Dorsal fin greyish-hyaline, the lappets dusky. Anal and pelvic fins hyaline, the caudal greyish with darker maculae on its proximal half.

Ecology. Habitat. The specimens examined came from trawl hauls in 2 localities near Nsadzi island. In both places the bottom is of mud and the depth of water between 70 and 180 feet.

Food. All the 25 specimens examined had been almost completely eviscerated by pressure change during capture, and in 16 of these specimens the remaining gut was empty. In the other 9 fishes at least part of the gut was intact and contained food,

namely: remains of *Caridina* sp. (Crustacea) in 5 specimens, very fragmentary and unidentifiable fish remains in 3, and a mixture of fish and crustaceans (probably *Caridina* sp.) in one other.

Breeding. All except one of the 25 specimens examined (129–229 mm. S.L.) are adult. The exceptional fish is an immature female 150 mm. S.L. (It should be noted that a female 129 mm. S.L. is adult.)

Diagnosis and affinities. In all respects, *H. dectocostoma* is very similar to *H. spekii* (see Greenwood, 1967).

Unfortunately, the live colours of *H. spekii* are unknown. But, judging from *post-mortem* coloration, *H. spekii* differs from *H. dectocostoma* in having a darker, more generally blue-grey ground coloration, and a dark (probably black) branchiostegal membrane. The preserved coloration of both species is similar, but again adult male *H. spekii* are darker and the branchiostegal membrane in *H. dectocostoma* is lighter.

On most morphometric criteria the two species are indistinguishable. The lower jaw of *H. dectocostoma* is more oblique than in *H. spekii* (30° – 40° , mode 35° , cf. horizontal to ca. 15°), and the posterior tip of the maxilla does not extend quite so far posteriorly (but there is some overlap interspecifically in this character).

The modal number of gill rakers in *H. dectocostoma* is higher (10 cf. 8), but the ranges overlap.

The least interorbital width in *H. dectocostoma* is slightly narrower than in *H. spekii* (20.0–23.1, $M = 21.6\%$ head, cf. 22.0–26.0, $M = 23.3\%$ in *H. spekii*), and the mean eye/preorbital ratio is lower (0.8–1.0, $M = 0.9$, cf. 0.8–1.3, $M = 1.0$).

Haplochromis dectocostoma also resembles *H. serranus* (see Greenwood, 1967, for a discussion of the *H. serranus*–*H. spekii* relationship, and Greenwood, 1962, for *H. serranus*). The resemblance includes an oblique lower jaw, but the species differ in such characters as their preserved coloration, the higher number of gill rakers in *H. dectocostoma* (10, cf. 8 or 9 in *H. serranus*), its deeper preorbital (19.4–23.8, $M = 21.7\%$ head, cf. 14.6–20.0, $M = 17.7\%$ in *H. serranus*), and its lower eye/preorbital ratio (0.8–1.0, $M = 0.9$, cf. 1.1–1.5, $M = 1.3$).

Phyletically, *H. dectocostoma* is a derivative of the *H. serranus* stem, and probably from a species anatomically indistinguishable from *H. spekii*.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
UGANDA		
B.M. (N.H.) 1968.8.30.292 (Holotype)	S. of Nsadzi isl. (180 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.302–309	N. and S. of Nsadzi isl. (70–160 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.293–301	S. of Nsadzi isl. (180 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.330–333	S. of Nsadzi isl. (180 feet)	E.A.F.F.R.O.

Haplochromis gilberti sp. nov.

(Text-fig. 33)

HOLOTYPE: an adult male 151.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.1) from near Bulago island.

The species is named in honour of Mr. Michael Gilbert, Experimental Fisheries Officer of the East African Freshwater Fisheries Research Organization. Michael Gilbert's enthusiasm and skill have added considerably to our knowledge of the Lake Victoria fishes, and especially the *Haplochromis* species from the deeper waters.

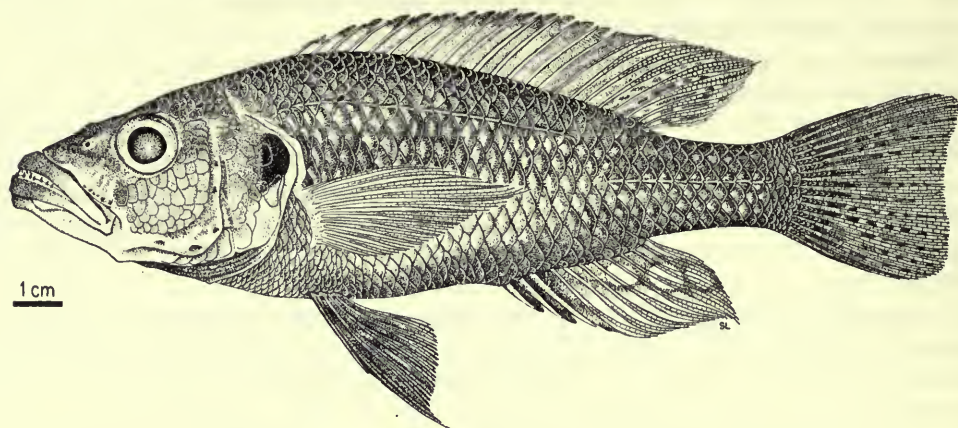


FIG. 33. *Haplochromis gilberti*. Holotype. Drawn by Sharon Lesure.

DESCRIPTION: based on 12 specimens (including the holotype) 125.0–150.0 mm. S.L. Depth of body 30.6–34.7 ($M = 32.3$) % of standard length, length of head 34.3–37.5 ($M = 36.0$) %.

Dorsal head profile straight or very slightly curved, sloping at an angle of 25° – 30° , its contour interrupted by the prominent premaxillary pedicels.

Preorbital depth 16.3–19.2 ($M = 17.8$) % of head, least interorbital width 17.0–19.6 ($M = 18.1$) %. Snout 1.0 (mode)–1.1 times as long as broad, its length 32.6–36.2 ($M = 34.4$) % of head, diameter of eye 23.0–27.5 ($M = 24.8$), depth of cheek 22.2–25.3 ($M = 23.7$) %.

Caudal peduncle 15.4–17.3 ($M = 16.6$) % of standard length, 1.4–1.6 times as long as deep.

Mouth slightly oblique (*ca.* 25°), jaws equal anteriorly or the lower projecting slightly. Lower jaw length 44.3–49.1 ($M = 47.5$) % of head, 1.9–2.3 (mode 2.0) times as long as broad; a distinct but low mental protuberance is developed. Pre-maxilla with its dentigerous surface somewhat expanded medially and anteromedially giving a slightly beaked effect. Posterior tip of the maxilla reaching a vertical through the anterior orbital margin or slightly beyond, rarely not quite reaching the level of the orbit.

Gill rakers: Nine (rarely 8 or 10) on the lower part of the first gill arch, the lower 1–3 rakers reduced, the upper 3–6 (usually 4) flattened, often anvil-shaped; the intervening rakers of varied shape, from relatively slender to relatively stout.

Scales: ctenoid. Lateral line with 32 (f.2) or 33 (f.9) scales; cheek with 3 or 4 rows. Five and a half (rarely) to 7 (mode $6\frac{1}{2}$) scales between the upper lateral line and the dorsal fin origin, 6 or 7 between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.5) or 25 (f.7) rays, comprising 15 spines and 9 or 10 branched rays. Anal with 11 (f.1) or 12 (f.11) rays, comprising 3 spines and 8 or 9 branched rays. Pectoral 24.0–29.9 ($M = 27.8$) % of standard length. Caudal truncate, scaled on its proximal half. Pelvics with the first ray produced (only one female is available).

Teeth. The *outer teeth* in *both jaws* are long, slender unicuspid, recurved distally. These teeth are well-spaced with 38–50 ($M = 40$) in the upper jaw.

The *inner teeth* are also unicuspid and curved, and are implanted obliquely, those of the lower jaw lying almost horizontally. There 3 or 4 irregular series of inner teeth in the upper jaw, and 2 or 3 series in the lower jaw.

Osteology. The *neurocranium* of *H. gilberti* is moderately elongate and slender, and except for its greater width across the interorbital region, resembles the type found in *H. tyrianthinus* and other members of the "*tridens*" species complex (see p. 51). Thus in general the skull of *H. gilberti* approaches the "*prognathus*" skull type (see Greenwood, 1967, p. 109 *et. seq.*). The cephalic lateral line tubes are moderately hypertrophied, with enlarged pores.

The *premaxilla* is moderately beaked. Together with the *dentary*, these bones can be considered typical of the condition found in many "*prognathus*"-group species.

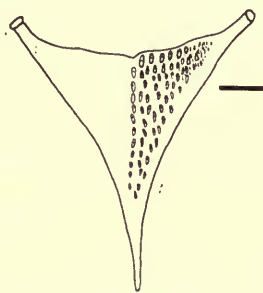


FIG. 34. *Haplochromis gilberti*. Lower pharyngeal bone. Scale equals 2 mm.

The *lower pharyngeal bone* (Text-fig. 34) is moderately slender, with its triangular dentigerous surface as long as broad. The teeth are coarse but compressed and cuspidate, and are arranged in 22–28 rows.

Coloration. The colours of live fishes are unknown.

Preserved material. *Adult males* are brownish-grey above the upper lateral line, on the dorsal surface of the head, the snout and the cheeks; silvery-grey below, the silver sheen most intense on the chest, belly and the operculum. The branchiostegal membrane is brownish, except for a faint dusky overlay in the opercular region of some individuals. In certain specimens there is a faint, dark lachrymal stripe, and faint traces of a dark midlateral longitudinal band.

The dorsal fin is dusky grey, the lappets black, the soft part with dark maculae. Caudal greyish, lighter along the posterior margin, the entire fin darkly maculate. Anal fin yellowish-hyaline, with a narrow, dusky base; the ocelli are large and dead-white. Pelvic fins are black.

Female (the only specimen available, an adult). Ground colour brownish grey above the upper lateral line, shading to silver below that level; a faint midlateral longitudinal stripe is visible on the flanks and caudal peduncle. The snout is greyish, the cheeks silvery, the branchiostegal membrane yellowish-white.

The dorsal fin is dark hyaline, as is the caudal which, however, is dusky at its base. The anal and pelvic fins are hyaline.

Ecology. Habitat. The species is so far known from only one locality, near Bulago island at a depth of 55–75 feet over a mud bottom.

Food. Two of the 12 guts examined were empty; of the others, 2 contained fragmentary remains of small cyprinid fishes, 1 unidentifiable fish remains, 2 fragmentary fish (cyprinid) and insect remains (chironomid pupae), 4 contained only fragments of chironomid pupae, and 1 an unidentifiable, colourless solid.

Breeding. Except for the single adult female (146 mm. S.L.), all the other specimens are adult males. The right ovary of the female is noticeably larger than the left one.

Diagnosis and affinities. Superficially (and in most aspects of its anatomy) *H. gilberti* resembles *H. paraguayarti* (see Greenwood, 1967, p. 69) and was probably derived from the same stem as that species. *Haplochromis gilberti* differs from *H. paraguayarti* principally in having a narrower interorbital (17.0–19.6, $M = 18.1\%$ of head, cf. 22.9–27.7, $M = 25.3\%$) and a lower mean number of outer teeth in the upper jaw (38–50, $M = 40$, cf. 42–62, $M = 54$ in *H. paraguayarti*); the outer teeth in *H. gilberti* are also more slender than those of *H. paraguayarti*.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.1 (Holotype)	Near Bulago isl. (55–75 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.2–12	Near Bulago isl. (55–75 feet)	E.A.F.F.R.O.

Haplochromis paraplagiostoma sp. nov.

(Text-fig. 35)

HOLOTYPE: an adult female 97.0 mm. S.L. (B.M. [N.H.] reg. no. 1968.8.30.127) from west of Bulago island, at a depth of 70 feet.

DESCRIPTION: based on 8 specimens (including the holotype) 90.5–98.0 mm. standard length.

Depth of body 34.1–38.7 ($M = 35.9$) % of standard length, length of head 31.9–33.4 ($M = 32.0$) %.

Dorsal head profile sloping at an angle of 35°–40°, almost straight but gently curved in the nuchal region, and with a slight supraorbital concavity.

Preorbital depth 15.5–18.7 ($M = 17.1$) % of head, least interorbital width 19.0–22.6 ($M = 20.9$) %. Snout 1.1–1.3 (mode 1.2) times as broad as long, its length 29.0–31.8 ($M = 30.2$) % of head, diameter of eye 24.1–29.0 ($M = 26.5$), depth of cheek 25.1–29.0 ($M = 27.3$) %.

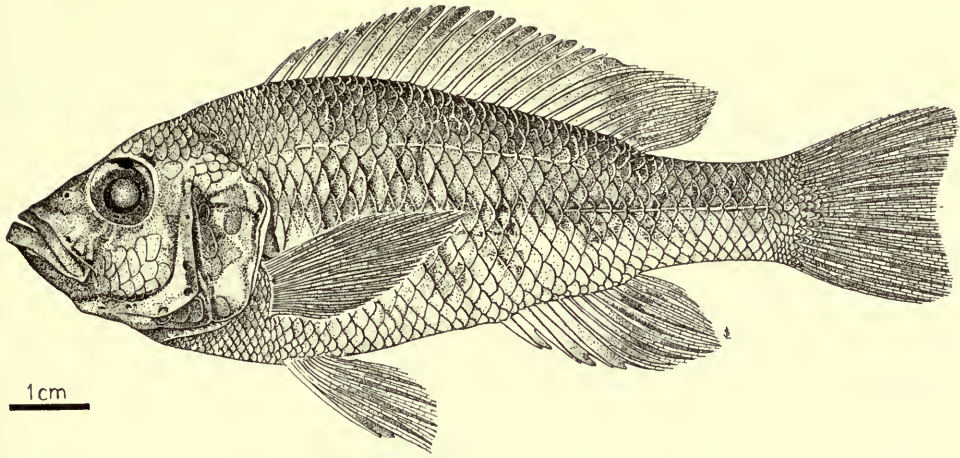


FIG. 35. *Haplochromis paraplagiostoma*. Holotype. Drawn by Sharon Lesure.

Caudal peduncle 17.6–20.4 ($M = 19.0$) % of standard length, 1.5–1.8 (mode 1.6) times as long as deep.

Mouth slightly oblique, sloping at an angle of 20° – 35° . Lower jaw projecting slightly, and with a distinct mental protuberance, its length 41.4–46.7 ($M = 44.3$) % of head, 1.6–2.0 times as long as broad. Premaxilla not expanded anteromedially. Posterior tip of the maxilla reaching a vertical passing through the anterior part of the eye.

Gill rakers: Nine (mode) or 10 on the lower part of the first gill-arch, the lower 1 or 2 reduced, the upper 2–4 flattened and branched, the intervening rakers relatively slender.

Scales: ctenoid. Lateral line with 32 (f.2), 33 (f.4), 34 (f.1) or 35 (f.1) scales; cheek with 3 or 4 rows. Six to $7\frac{1}{2}$ (mode 6) scales between the upper lateral line and the dorsal fin origin, 6 or 7 (mode) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 rays, comprising 15 spines and 9 branched rays. Anal with 11 (f.5) or 12 (f.3) rays, comprising 3 spines and 8 or 9 branched rays. Pectoral 24.5–28.0 ($M = 26.7$) % of standard length. Caudal truncate, scaled on its proximal half to two-thirds. Pelvic fins with the first and second branched rays produced, the first more so, but without any sexual correlation.

Teeth. *Outer row*. In most specimens the outer teeth in both jaws are relatively compressed and unequally bicuspid, with a few weakly bicuspid and a few slender unicuspid interspersed amongst them. In the largest fish (98.0 mm. S.L.) unicuspid teeth predominate. Posteriorly in the *upper jaw* the teeth are smaller, and in some specimens are finer than the lateral and anterior teeth; unicuspid or weakly bicuspid teeth are usual in this region of the jaw. Teeth in the *lower jaw* are relatively stouter than those in the upper jaw, the discrepancy being most marked anteriorly and anterolaterally.

There are 60–72 ($M = 64$) outer teeth in the upper jaw.

The *inner teeth* are all tricuspid, very obliquely implanted, and arranged in 2 rows in the upper jaw, and in 1 or 2 rows in the lower jaw.

Osteology. No complete skeleton is available. The *lower pharyngeal bone* is slender, with its triangular dentigerous surface slightly broader than long. The teeth are fine, compressed, and cuspidate and are arranged in about 30 rows.

Coloration. The colours of *live fishes* are unknown.

Preserved material. There is so little sexual dimorphism apparent in the preserved coloration of the sample available that a combined description of the sexes can be given.

The ground coloration is light pinkish-brown; scales on the dorsal aspects of the body, on the flanks and on the upper part of the belly have dark margins, thereby giving the whole body a faintly reticulate pattern. Scales along the midlateral line have broader dark margins, thus producing an ill-defined, sometimes interrupted longitudinal stripe from behind the operculum to the caudal fin origin. In some fishes there are very faint traces of 5-7 vertical bars on the flanks. The preorbital region of the head is dark, as is the interopercular region, the posterior margin of the preoperculum and at least part of the branchiostegal membrane; a faint lachrymal stripe is visible in all specimens.

The dorsal and anal fins are hyaline to greyish, the former with dark lappets. In males the anal fin has two indistinct ocelli, faintly outlined anteriorly in black. Caudal greyish, faintly maculate in some individuals. Pelvic fins dark in both sexes, but more uniformly so in males.

Ecology. All 8 specimens came from the same locality near Bulago island, over a mud bottom at a depth of 70 feet.

No information was obtained on the feeding habits of *H. paraplagiostoma*.

Some difficulty was experienced in determining the sexual state of several specimens; all except one (a ripening female, 93 mm. S.L.) could be either juvenile or quiescent.

Diagnosis and affinities. There is a certain superficial similarity between *H. paraplagiostoma* and *H. plagiostoma* (see Greenwood, 1962, p. 199), but the species differ in a number of characters, including the dentition. For example *H. paraplagiostoma* has a shorter head (31.9-33.4, $M = 32\%$ standard length, *cf.* 34.0-37.5, $M = 36.0\%$), shallower cheek (25.1-29.0, $M = 27.3\%$ head, *cf.* 28.0-36.8, $M = 33.0\%$), shallower preorbital (15.5-18.7, $M = 17.1\%$ head, *cf.* 18.0-21.5, $M = 19.8\%$) and a shorter lower jaw (41.4-46.7, $M = 44.3\%$ head, *cf.* 44.0-54.5, $M = 49.2\%$); the lower jaw of *H. paraplagiostoma* also slopes less steeply than that of *H. plagiostoma*.

The dentition differs in that the outer teeth of *H. plagiostoma* at all known lengths (69-147 mm. S.L.) are unicuspid, short, and strongly curved whereas in specimens of *H. paraplagiostoma* < 96 mm. S.L. the majority of teeth are distinctly and very unequally bicuspid, and are weakly curved. Unicuspid teeth are not frequent in fishes below 96 mm. S.L., and in the larger fish the unicuspid teeth differ in shape and relative size from those of *H. plagiostoma*.

There are clear-cut differences in the preserved coloration of the two species (*cf.* above and p. 201 of Greenwood, 1967).

Despite the superficial resemblances between *H. paraplagiostoma* and *H. plagiostoma*, we are not inclined to think that they indicate close relationship between the species.

Until more is known about *H. paraplagiostoma* the species cannot readily be linked with any of the known deep-water or inshore dwelling *Haplochromis* species. However, in many respects *H. paraplagiostoma* shows some affinity with the organizational level seen in *H. empodisma*. We do not imply that the species are closely related, but rather that *H. paraplagiostoma* could have evolved from a *H. empodisma*-like stem (see Greenwood, 1960).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1968.8.30.127 (Holotype)	W. of Bulago isl. (70 feet)	E.A.F.F.R.O.
B.M. (N.H.) 1968.8.30.128-134	W. of Bulago isl. (70 feet)	E.A.F.F.R.O.

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APPENDIX

Haplochromis obesus (Blgr.) 1906

Six small fishes (67.0-71.0 mm. S.L.) caught at a depth of 80-90 feet over a mud substrate north of Nsadzi island, are tentatively identified as *H. obesus*. This species is otherwise known from littoral and immediately sublittoral habitats.

Our identification of these fishes is based on their peculiar dentition and their general facies, both of which are typical for *H. obesus* (see Greenwood, 1959). In most morphometric characters (see table below) the specimens agree with *H. obesus*, except for having a narrower interorbital (mean width 24.6% of head, cf. 32.2% in *H. obesus*) and a slightly longer caudal peduncle. Some of the Nsadzi fishes have a higher number of gill rakers (11) than is modal for *H. obesus* (9 or 10); however, a few *H. obesus* also have counts of 11, and one of the Nsadzi specimens has 10 gill rakers.

All six Nsadzi fishes (5 males, 1 female) are adult and sexually active. By contrast, the smallest known adult *H. obesus* from inshore and sublittoral populations is 85.0 mm. S.L. (Greenwood, 1959).

Another biological difference between the Nsadzi and the other populations concerns food. Three of the six Nsadzi fishes contained ingested material in the

stomach which, in each instance, is packed with Cladocera and Copepoda. The food of individuals from inshore habitats appears to be the embryos and larvae of fishes, especially Cichlidae (Greenwood, *op. cit.*). The significance of this dietary difference is impossible to assess. In neither instance are large numbers of gut analyses available (3 from Nsadzi, 18 from other habitats), and furthermore, all the Nsadzi fishes are smaller than any of the inshore fishes examined.

This marked size difference also hampers evaluation of the observed discrepancies in certain morphometric characters (see above); only one specimen of the Nsadzi sample falls within the size range of other *H. obesus* material.

Partly for this reason, and partly because we have so few deep-water specimens, we do not feel justified in creating a new species for the Nsadzi fishes.

The principal morphological characters of the Nsadzi specimens may be summarized as follows:

S.L.	D.*	H.*	Po. %	Io. %	Snt. %	Eye %	Ck. %	Lj. %	C.P.*
67.0	34.3	31.3	14.3	23.8	28.6	33.3	23.8	47.6	17.9
69.0	34.3	33.3	13.0	23.9	28.3	30.4	21.8	43.6	18.9
69.0	35.2	33.3	13.0	26.1	28.3	28.3	21.8	43.6	18.9
70.0	34.3	31.4	15.8	22.7	28.6	31.8	25.0	45.4	17.8
70.0	37.1	32.9	15.2	26.1	30.5	30.5	23.9	43.5	17.2
71.0	34.5	33.1	17.0	25.5	28.9	29.9	23.4	46.9	18.4

* = % of standard length
% = % of head

The lower jaw is 1.4–1.9 times as long as broad; the snout 1.3–1.6 times as broad as long. The caudal peduncle is 1.4–1.6 times as long as deep.

Gill rakers: short and stout, the upper 2 or 3 flattened and anvil-shaped; 10 (f.1) or 11 (f.5) on the lower part of the first gill arch.

Teeth. The *outer row* in the *upper jaw* is composed of 30–38 ($M = 36$), unicuspid or weakly bicuspid, slightly recurved teeth. In the *lower jaw*, the outer teeth are unicuspid (a few weakly bicuspid in one fish), with the tips of the anterior and antero-lateral teeth directed outwards.

The *inner teeth* are tricuspid in the upper jaw, unicuspid in the lower, and are arranged in 1 or 2 rows.

Fins. Dorsal with 15 (f.3) or 16 (f.3) spines, and 8 or 9 branched rays. Pectoral 27.1–31.0 % of standard length.

Scales: ctenoid. Lateral line with 30 (f.2), 31 (f.2) or 32 (f.2) scales, cheek with 3 rows. Five and a half or $6\frac{1}{2}$ scales between the dorsal fin origin and the upper lateral line, 6 between the pelvic and pectoral fin bases.

Register numbers: B.M. (N.H.) 1968.8.30.329; and 1968.9.3.3–7.

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FINE STRUCTURE OF
GROMIA OVIFORMIS
(RHIZOPODEA : PROTOZOA)

R. H. HEDLEY & J. ST. J. WAKEFIELD



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SYNOPSIS

Four shell-components are recognized—the outer wall, honeycombed membranes, fibrillar material and oral capsule. The outer wall is proteinaceous and finely fibrillar, with an outer electron-dense layer characterized by a high polysaccharide content. The whole structure is perforated at intervals by wall canals whose possible functions are discussed. The honeycombed membranes have an hexagonal architecture, and in cross section appear striated; the relationship of the striations to the hexagonal structure is illustrated. The oral capsule is composed mainly of polysaccharide microtubules, and its junction with the other shell-components is described. The significance of the amino acid hydroxyproline being present in the shell is discussed. A conventional plasma-membrane occurs below the fibrillar material of the shell.

The cytoplasmic organelles discussed in detail include the microbodies, Golgi apparatus, secretion granules and nuclei. Microbodies have a variable morphology and a simple tubular nucleoid. The Golgi apparatus is considered to be concerned with the manufacture of wall-material. The pseudopodia are characterized by the absence of organelles or any other recognizable structures; they are limited by a plasma-membrane and contain ground plasm.

Gametes possess a single mucronate flagellum, a single nucleus, two basal bodies, mitochondria, fat droplets and two enigmatic organelles.

INTRODUCTION

THE widely-distributed, shallow-water, marine rhizopod *Gromia oviformis* Dujardin, 1835, has attracted the attention of protozoologists because of its relatively large size—up to 5 mm.—uncertain systematic position (Arnold, 1952; Hedley, 1958) and suggested similarity to some of the Chitinozoa, a palaeozoic group of fossils (Collinson & Schwalb, 1955; Hedley, 1962).

The present paper is a detailed account of the fine structure of the adult organism and the gamete and it clarifies certain problems of shell-structure raised by Hedley (1960) and Hedley & Bertaud (1962).

MATERIAL AND METHODS

Live animals were collected from the intertidal zone at Wembury Bay, Plymouth, England, where they live in abundance attached to protected rock-faces or the hold-fasts of *Laminaria*. After collection they were placed in Foyn's Erdschreiber medium (Arnold, 1954) in plastic containers, 2 inches in diameter, and kept at room temperature, 18–20° C. Under these conditions animals live for up to 6 months, but do not appear to feed or grow despite being offered various flagellates and diatoms. Some animals, shortly after collection, liberated gametes.

Electron microscopy.—Gametes for shadowed whole-mounts were prepared by the method described by Manton (1964), in which a drop of sea-water containing gametes is placed on a carbon-coated grid. A petri-dish containing a few drops of 2% osmium tetroxide is inverted over the grid for 1½–2 minutes. The vapour fixes the gametes, which fall onto the carbon film; the excess liquid is removed with filter paper and the grid is allowed to dry. The salt deposit is removed by several washes of distilled water and the grid is dried again. These preparations are shadowed with gold/palladium at an angle of approximately 30°. For the examination of gamete ultrastructure the creamy peripheral layer of cytoplasm, characteristic of an animal about to liberate gametes, is pipetted off and squirted into fixative. After fixation the gametes are centrifuged to form a pellet, and in subsequent procedures they are handled as a single piece of tissue. The standard fixing and embedding procedure used for both gametes and adult animals is as follows. Specimens are fixed in 4% glutaraldehyde in 0.1 M cacodylic acid buffer with 0.25 M sucrose, and post-fixed in Caulfield's osmium tetroxide. After rapid ethanol dehydration, specimens were embedded in Epon 812. For preservation of pseudopodia the following fixatives were used: Palade's osmium tetroxide; Caulfield's osmium tetroxide; 2% osmium tetroxide in sea-water; 2% osmium tetroxide in 0.2 M cacodylic acid buffer with 0.4 M sucrose; 4% glutaraldehyde in sea-water followed by 2% osmium tetroxide in sea-water; 4% glutaraldehyde in 0.15 M cacodylic acid buffer with 0.3 M sucrose followed by 1% osmium tetroxide in 0.15 M cacodylic acid buffer with 0.4 M sucrose and 0.3 M glucose; 5% acrolein in 0.2 M phosphate buffer with 0.3 M sucrose followed by 1% osmium tetroxide in 0.2 M phosphate buffer with 0.3 M

sucrose and 0.2 M glucose; and the picric acid-formaldehyde mixture of Stefanini *et al.* (1967). Sections were cut with a diamond knife on a Porter-Blum ultramicrotome, stained with a saturated alcoholic solution of uranyl acetate followed by Reynold's lead citrate. For the demonstration of polysaccharide the methods of Rambourg (1967) and Thiery (1967) were used. Sections were examined on an A.E.I. EM 6B microscope operating at 60 kV, and recorded on Ilford N50 plates.

Amino acid analysis.—Approximately 3,000 specimens were used. After being picked off rock-surfaces, whole animals were placed in distilled water so that the resultant osmotic effect caused most of the cytoplasm to be squeezed out of the shell. Each empty shell was cut into two or three pieces and placed for two hours in an ultrasonic cleaner. Several shells were embedded for electron microscopy, and on examination the outer wall and honeycombed membranes were still intact, while all contaminating material had been removed. The clean shells were ground with powdered glass in either 6N/HCl or saturated Ba(OH)₂. Extracts from both were prepared by standard hydrolysis procedures and subjected to two dimensional chromatography on thin-layer silica gel plates, using the following solvent systems: (a) *n*-butanol: acetic acid: water (60 : 20 : 20)/phenol; (b) chloroform : methanol : 17% ammonia (2 : 2 : 1)/phenol. The chromogenic agent used was ninhydrin. After reference to standard maps comparable mixtures of amino acids were prepared and run in parallel with the extracts.

SHELL

Previous work.—The shell of *Gromia* was first described by Bütschli (1894), who noted that the single opening could be closed by the collar. A more detailed description by Awerinzew (1903) indicated that the wall was a two-layered structure, with an outer perforate and an inner structureless layer. Jepps (1926) confirmed this description, adding that the outer perforate part of the wall was composed of a mosaic of irregular prismatic rods, and was resistant to hydrolysis. She concluded from a number of tests that the wall was composed of pseudochitin, a term introduced by Awerinzew (1907) when describing the composition of fresh-water testacean shells. Apart from a text-figure by Jepps (1926), showing the junction between wall and oral capsule, the relatively complex oral region had not been studied until Arnold (1952) published a diagram of a dissected oral region. The shell was next described as a single-layered radially perforate tectinous structure, with the inner structureless layer of previous authors being interpreted as a layer of non-granular cytoplasm (Hedley, 1960). The same author described the oral region in detail and gave an account of the opening and closing movements of the oral capsule. The shell was considered to be composed of mucoprotein with an unexpected high content of organically bound ferric iron, whilst the oral capsule was shown to be predominantly acid mucopolysaccharide. Hedley & Bertaud (1962), in a study of shell ultrastructure, confirmed the perforate nature of the outer wall, and described the fine structure of the wall as having a sponge-like texture. They also reported a unique system of honeycombed membranes, but did not locate a conventional plasma membrane between the cytoplasm and the shell. The oral capsule was shown to be made up

of a mass of microtubules arranged in a well-organized but complex pattern. Some of the problems which arose from the work of Hedley & Bertaud (1962) are considered in the present account. These include the relationship between the oral capsule and the shell-wall, the function of the canals which perforate the wall, the position of the plasma membrane, and the position of the bound ferric iron.

The component parts of the shell, which are recognized and discussed in the present paper, are, beginning from the exterior, the outer wall invested by an electron-dense layer, the honeycombed membranes, the fibrillar material, and in the oral region the oral capsule (Text-fig. 1, Pl. 2, fig. A, Pl. 3, fig. A).

Outer wall.—The wall is composed of a mass of fine fibres 5–6 nm. thick (Pl. 3, fig. B), and is perforated at intervals by wall canals (Pl. 2, figs. B and C). In cross sections of the wall the fibres are aligned parallel to the shell-surface (Pl. 3, fig. B). In tangential section the fibres are arranged at random, except in the vicinity of wall canals where they are arranged concentrically around the canal to a depth of about $0.1\ \mu\text{m}$ (Pl. 2, fig. B).

The electron-dense points, 4 nm. in diameter, visible in cross sections are probably fibres running at right angles to the plane of section, rather than condensations of some other electron-dense material. The concentration of these points along the edge of the canals in longitudinal section (Pl. 2, fig. C), where many of the fibres are at right angles to the plane of section (Pl. 2, fig. B), is consistent with this view.

The outer surface of the wall is limited by a strongly electron-dense layer, 10–16 nm. thick (Pl. 2, figs. A and C, Pl. 3, figs. A and B). In an attempt to determine the origin of this electron density some animals were fixed in glutaraldehyde, not post-fixed in osmium tetroxide, and not stained with uranyl acetate or lead citrate after sectioning. In these, the outer layer was still electron dense, but less so than in normally-prepared sections, indicating that the electron density is not entirely due to introduced heavy metals, and consequently not entirely due to the presence of unsaturated fatty acid (Korn, 1966). Earlier studies have shown that the outer wall of *Gromia* has a high content of bound ferric iron (Hedley, 1960). The modification of Perl's method for ferric iron in electron microscopy (Thiéry, 1962) was used to see if the iron was concentrated in the outer electron-dense layer. Unfortunately, in this laboratory, the method does not produce satisfactory results, as an even precipitate is deposited on the section over both the specimen and embedding medium. However, the electron density present in specimens which had not come into contact with heavy metals during preparation indicates that the electron-dense layer may have a high content of ferric iron. Using the silver methenamine stain of Rambourg (1967), and Thiéry (1967), the electron-dense outer layer reacts positively for polysaccharide (Pl. 6, fig. B).

Canals which perforate the outer wall are present throughout the shell and are not restricted to any particular area. In cross section they are usually circular, 0.2 – $0.3\ \mu\text{m}$ in diameter (Pl. 2, fig. B) and vary from straight cylinders to irregular passages with extensive blind cisternae. The canals open freely on the inner surface of the outer wall (Pl. 2, fig. C), but the opening on the outer surface is reduced to a small pore (Pl. 3, fig. B and D). The pore, approximately 85 nm. in depth and 35 nm. in diameter, is formed by an open-ended invagination of the outer electron-dense

layer. The function of the wall-canals is still unresolved, although the suggestion by Hedley & Bertaud (1962)—that they are pores through which cytoplasm can pass—now appears to be untenable. The cytoplasm lies beneath the honeycombed membranes, and to have access to the outside through the wall-canals, it would be

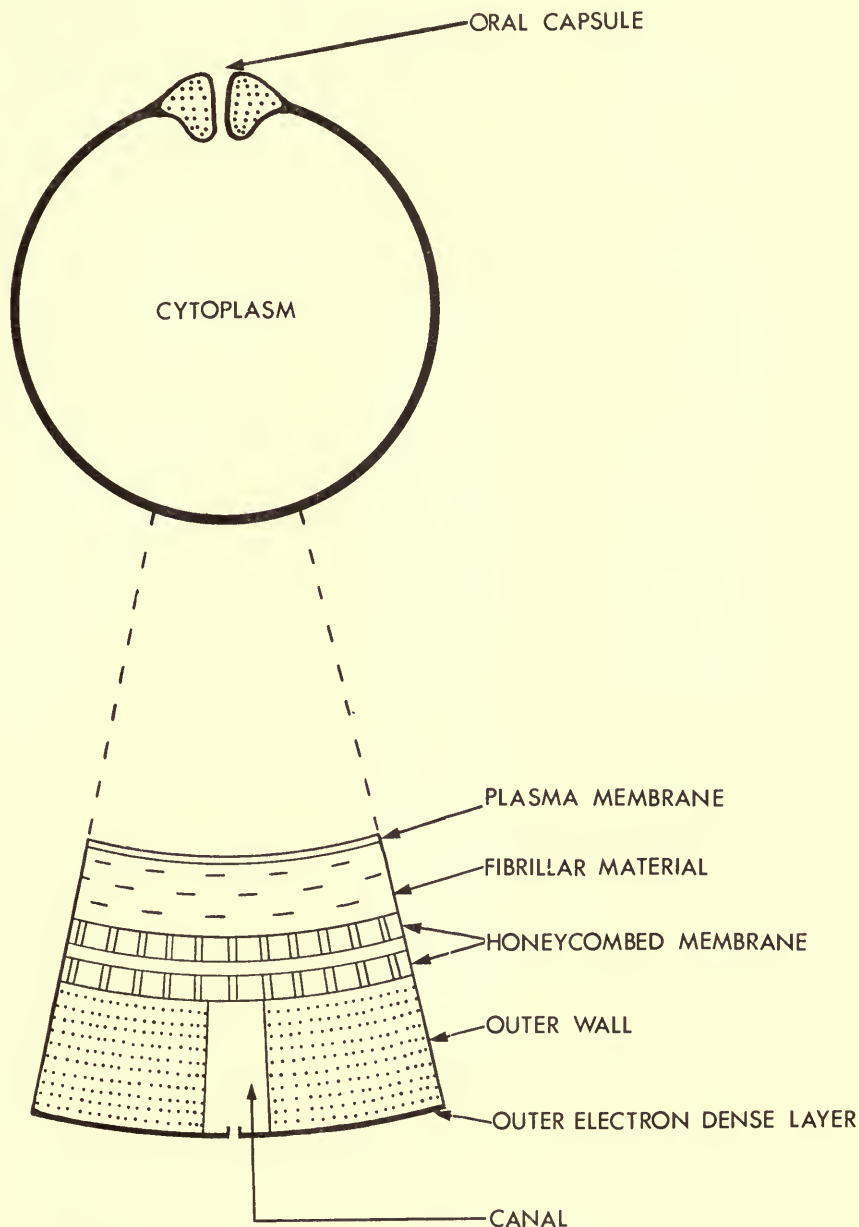


FIG. 1. Diagram of the shell of *Gromia oviformis* showing the position of the oral capsule and details of wall-structure discussed in the text.

necessary to have gaps in the honeycombed membranes. These have not been seen, and cytoplasmic material has not been detected in the wall-canals. Another possible function of the wall-canals is to allow the release of gametes to the exterior. Adults are often half buried in mud and debris, which is loosely cemented together, with the oral region attached firmly to the substrate. During gametogenesis the cytoplasm separates from the stercomata and xanthosomes which occupy the lower half of the shell, the maturing gametes developing in the upper half (Hedley, 1962). In this position there is no escape route for the gametes through the mouth and the wall-canals could provide a possible exit. The head of the gametes, however, measure $2-3\text{ }\mu\text{m}$ while the wall canals are only $0.2-0.3\text{ }\mu\text{m}$, moreover the honeycombed membranes separate the gametes from the outer wall. The passage of gametes through the honeycombed membranes and wall-canals could be facilitated by enzyme action partially breaking down the honeycombed membranes and outer wall at gametogenesis. This suggestion is supported by the observation that shells of animals which have undergone gametogenesis are much weaker than normal and less strong than those shells of heat-killed animals, which have been left in non-sterile sea-water for many months (Hedley, 1962).

Honeycombed membranes.—Moving inwards from the outer wall the next component of the shell is the complex of honeycombed membranes (Text-fig. 1, Pl. 2, fig. A, Pl. 3, fig. A). These lie parallel to the outer wall in sheets, measuring $20-50\text{ nm}$. thick and $7-15\text{ }\mu\text{m}$ across, forming an interleaved stack of up to 15 membranes. The structure of a membrane is best seen in tangential section, which gives a plan view (Pl. 4, fig. A). The membrane is composed of an hexagonal array of cylinders $10-20\text{ nm}$. in diameter, with a wall-thickness of $2-2.5\text{ nm}$., spaced 10 nm . apart. Each cylinder is connected to the six surrounding cylinders by a septum $2-2.5\text{ nm}$. thick, in the middle of which is an electron-dense spot $3-4\text{ nm}$. Occasionally a tangential section may contain more than one membrane. When this occurs the simple hexagonal pattern of each interacts producing Moiré patterns (Pl. 3, fig. C). Similarly produced Moiré patterns have been described from negatively stained bacterial membranes (Glauert, 1966).

When cut in cross section (Pl. 2, fig. A, Pl. 3, fig. A, Pl. 4, fig. B) the membranes appear as banded ribbons $20-50\text{ nm}$. thick. Four types of banding may be distinguished: Type 1. An alternating sequence of $10-12\text{ nm}$. thick light bands and $7-8\text{ nm}$. thick dark bands, with an interperiod length of 20 nm . (Pl. 3, fig. A); Type 2. An interperiod length of 20 nm . composed of the following sequence; dark 3.5 nm ., light 6.5 nm ., dark 3.5 nm ., light 6.5 nm . (Pl. 3, fig. A). That the repeated period is 20 nm . rather than 10 nm . composed of dark 3.5 nm ., light 6.5 nm . bands is difficult to detect and is due to every second light band being slightly less electron dense than every first light band; Type 3. An interperiod length of 6 nm . composed of alternating light and dark bands 3 nm . thick (Pl. 4, fig. B); Type 4. An homogeneous non-banded ribbon (Pl. 3, fig. A). The banding pattern is constant throughout the length of any one membrane. The frequency of occurrence of banding patterns estimated from an examination of all available micrographs is approximately, type 1, — 50%, types 2 or 3, — 45%, and type 4, — 5%.

The banding patterns produced in membrane cross sections are due to the arrange-

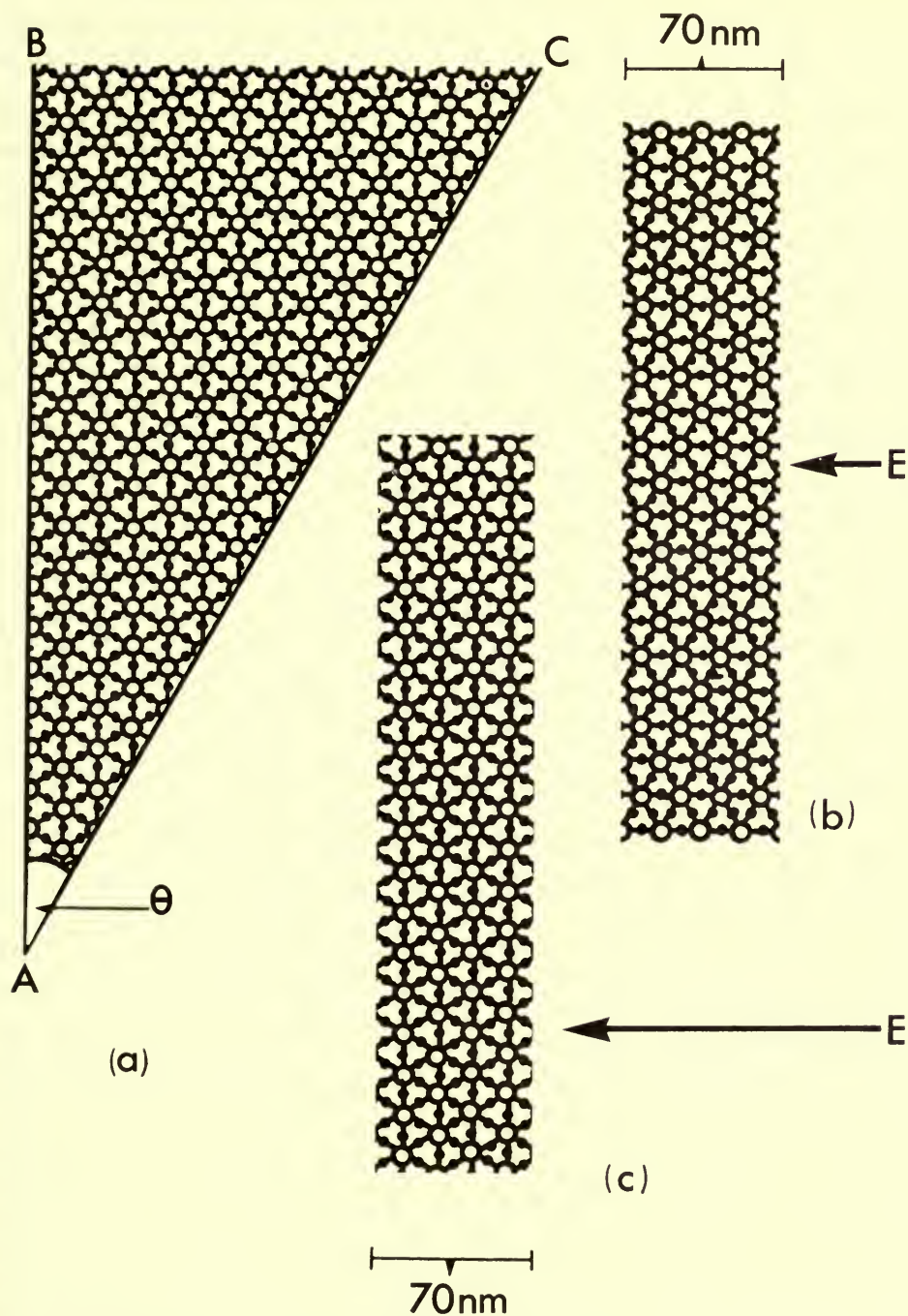


FIG. 2. Plan view of a honeycombed membrane: for discussion see text. E, indicates the direction of the electron beam.

ment of the cylinders in that section, and can be related to the plan view of the membrane in the following way. In plan view the cylinders are arranged in a strict hexagonal array (Pl. 4, fig. A). There are three axes of symmetry with a 60° angle between each. Each 60° segment is identical and bordered by two axes, and can be divided into two symmetrical halves 30° each (Text-fig. 2a). When a membrane is cut in section the direction of section is at a constant angle to the axes throughout the extent of that membrane. If an average section thickness of 70 nm. is assumed (Williams & Meek, 1966), then Text-fig. 2b represents a plan view of such a section in the direction of AC (Text-fig. 2a) i.e. the bisector of a 60° segment. When this is viewed in cross section, in the electron microscope, the membrane appears as an alternating sequence of dark and light bands, i.e. type 1 banding pattern (Pl. 3, fig. A). That this banding is due to the arrangement of the cylinders, is clearly seen in Pl. 4, fig. C. When the angle θ decreases (Text-fig. 3a and c—a section in the direction AB where $\theta = 0^\circ$) the banding pattern will change and one of the types 2, 3 or 4 will be produced. The particular arrangement of cylinders which produces any of these banding patterns has not been deduced.

Fibrillar material.—The outer wall, honeycombed membranes and plasma membrane are sometimes in close contact, but more usually they are separated from each other by a fine fibrillar substance (Pl. 2, fig. A, Pl. 3, fig. A). This is morphologically similar to that material comprising the outer wall and occurring in the wall-canals. Further, there is a more dense amorphous substance, which may be either condensations of the fibrillar material or an entirely different substance. The function of this material is unknown, although part of the fibrillar material may be a precursor of the outer wall. There is often a region on the inner face of the outer wall which is slightly more electron dense than the rest of the wall (Pl. 2, fig. C), and this is presumably the zone of accretion. It is unlikely that the wall grows by addition of material to the outer surface, because in *Gromia* there is no extramural layer of cytoplasm bathing the shell, as there is in allogromoid foraminifera (Hedley, 1964).

Amino acid composition.—The following amino acids were detected; alanine, arginine, aspartic acid, glutamic acid, glycine, hydroxyproline, leucine/iso-leucine, lysine, ornithine, phenylalanine, proline and valine. The somewhat surprising presence of hydroxyproline was checked and confirmed. Hydroxyproline is usually considered to be an amino acid unique to the skeletal protein collagen. There are, however, some exceptions to this generalization. One is in certain plant cell-walls which are non-collagenous and where hydroxyproline comprises 13% of the amino acids present (Lamport & Northcote, 1960). A second probable exception occurs in the nematocytes of both *Hydra* and *Physalia*, where a hydroxyproline content of 22–31% is reported (Lenhoff *et al.*, 1957, Lenhoff & Kline, 1958), and where in *Hydra* collagen has not been demonstrated by electron microscopy (Slautterbach, 1963). As there is no collagen demonstrable in the fine structure of the shell of *Gromia*, the hydroxyproline almost certainly originates from a non-collagenous protein. Another possibility, although somewhat unlikely, is that the honeycombed membranes are composed of a collagen with an atypical fine structure. A collagen organized in an hexagonal pattern has been described by Jakus (1956). This is Descemet's membrane from the inner surface of the cornea of a variety of vertebrates. The

filaments making up this membrane do not possess the typical banded pattern of collagen, but their collagenous nature has been established by chemical analysis and x-ray diffraction. There are considerable differences between this membrane and those found in *Gromia*: the spacing of the hexagonal lattice in Descemet's membrane is 100 nm., whilst in the honeycombed membranes in *Gromia* it is 20 nm.; the nodes where the axes join in Descemet's membrane are solid, in the honeycombed membranes they are hollow cylinders; in Descemet's membrane the individual lamellae are less than 5 nm. thick, in the honeycombed membranes they are 30 nm. thick. If the honeycombed membranes are collagenous, it is difficult to see how the tropocollagen molecule (300 by 5 nm.) makes this hexagonal pattern where the longest straight length is only 10 nm.

Oral capsule.—The extracellular oral capsule is composed of outer wall material enclosing a mass of microtubules (Text-fig. 2, Pl. 5). There is no definite junction between wall and oral capsule, the most obvious change in the region being the disappearance of the honeycombed membranes (Pl. 5). The outer wall thickens and bifurcates, the main part going along the outer face of the oral capsule, the much smaller branch lining the inner face. Between the two branches, where they divide, there is a thickening of outer wall material. The extension of the wall along the outer surface of the oral capsule covers approximately two-thirds of the capsule. Near its edge the outer wall tapers to a point and the outer surface is crenated. The thinner extension of the wall along the inner surface of the oral capsule also continues for about two-thirds of the length of the capsule. It is these two extensions of the outer wall which stain strongly with certain basic dyes (Hedley, 1960, fig. 2F).

The strongly electron dense layer (Text-fig. 3, Pl. 5), is prominent in the oral capsule; it lines both surfaces of the outer extension of the outer wall, and it lines most of the microtubular mass. In the region of the microtubular mass, between the end of the electron-dense layer and the end of the outer wall extension, there is a 1 μ m thick layer composed of a poorly-defined fibrillar material (Pl. 4, fig. D). The fibrillar material of the shell lines the base of the oral capsule at the end of which it merges with a similar layer lining the pseudopodia.

The main part of the oral capsule is composed of microtubules 25–30 nm. in diameter and of filaments 5–6 nm. thick which lie between the tubules (Pl. 4, fig. D). When the capsule is cut in vertical section (Text-fig. 3, Pl. 4, fig. D) the microtubules are always cut in cross section. When the capsule is cut tangentially the tubules are cut in tangential section and are arranged in a chevron pattern (Pl. 6, fig. B). A three dimensional reconstruction of the arrangement of the microtubules from this evidence has not been possible, but the predominant direction of the tubules is circumoral. This microtubular part of the oral capsule is mainly acid mucopolysaccharide with little or no lipid or protein (Hedley, 1960). Using the silver methenamine technique (Rambourg, 1967) both the microtubules and fibrils stain strongly, indicating a polysaccharide composition (Pl. 6, fig. B). Although the microtubules are morphologically similar to cytoplasmic microtubules described from animal and plant cells (Porter, 1966) they are basically quite different. The microtubules of the oral capsule are extracellular, cytoplasmic microtubules are intracellular. Cytoplasmic microtubules are proteinaceous (Shelansky & Taylor, 1967), those of the

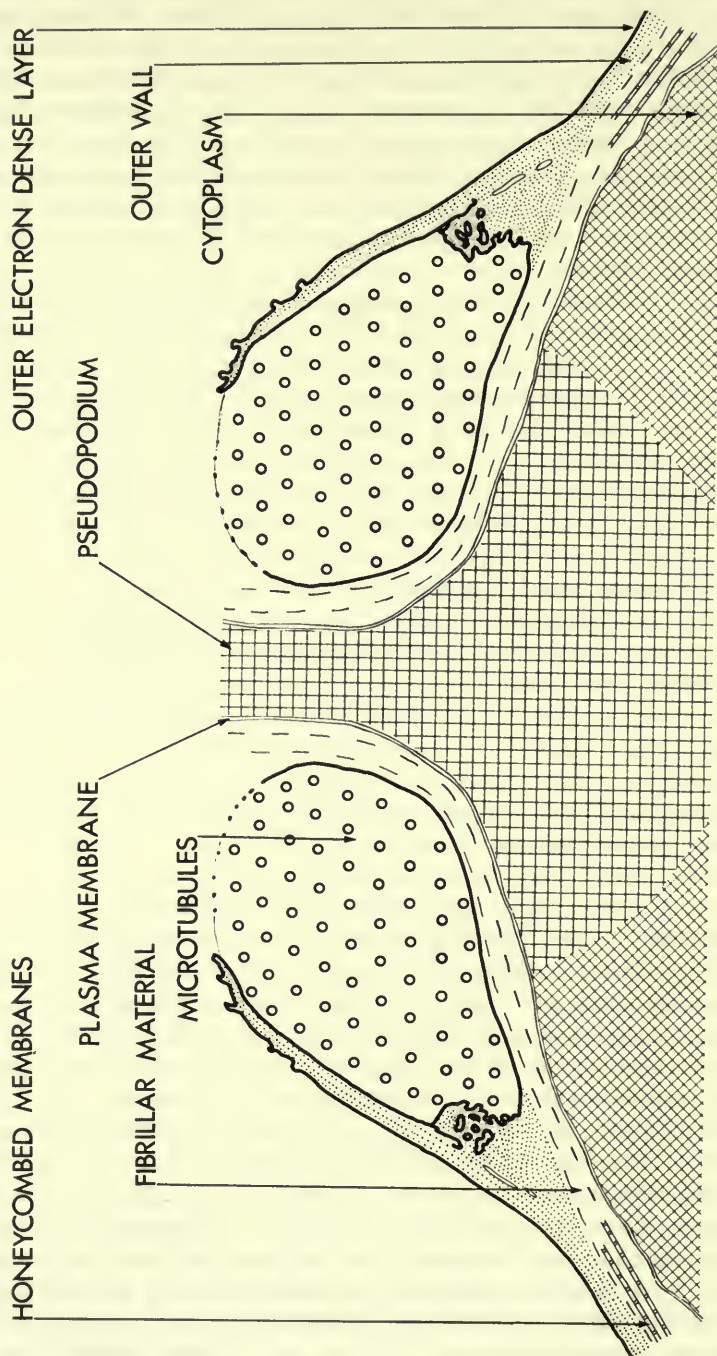


FIG. 3. Diagram of the oral capsule and opening through which pseudopodia are extruded.

oral capsule are composed of polysaccharide. The substructure of the microtubules in the oral capsule is unknown, and it is not possible to compare them, at this level, with cytoplasmic microtubules whose substructure has been resolved (Behnke & Zealander, 1967).

CYTOPLASM

Previous work.—Several protozoologists have described some aspects of the cytoplasmic structure of *Gromia* (Reichert, 1865, Schultz, 1866, Rhumbler, 1894, Bütschli, 1894, Schaudinn, 1894, Zarnik, 1907, Awerinzew, 1910), but it was Jepps (1926) who made the first general study. The next account of importance was concerned primarily with fine structure (Hedley & Bertaud, 1962). This, like other studies which had preceded it, was hampered by difficulties inherent in sectioning the animal, due to the presence of brittle xanthosomes and ingested sand-grains. Inadequate fixation has also limited the results obtained from previous investigations. Consequently certain features of cytoplasmic organization have remained unresolved, and further investigation of these, in particular the structure and position of the plasma membrane, the fine structure of the pseudopodia and general cytoplasmic ultrastructure, has been the chief aim of the present study.

Plasma-membrane.—A conventional plasma-membrane (Robertson, 1963) was not detected by Hedley & Bertaud (1962), and they suggested that the honeycombed membranes might be an unusual form of plasma-membrane. Later, this possibility was extended when it was suggested that the honeycombed membranes might represent a high permeability state of a normal cell-membrane in response to chemical or physical stimulus (Bertaud & Hedley, 1963). This view was expressed in the light of normal and conventional cell-membranes of red cell ghosts proving to have an hexagonal architecture after saponin treatment (Dourmashkin *et al.*, 1962). Kavanau (1963, 1965) has also suggested that the honeycombed membranes in *Gromia* may be a plasma-membrane, interpreting them, with reference to his membrane model system, as membranes fixed in the open configuration (Kavanau, 1963). These postulations are now shown to be incorrect as a conventional plasma-membrane is now demonstrated, lying below the honeycombed membranes (Pl. 2, fig. A, Pl. 3, fig. A, Pl. 8, fig. C). The membrane is tripartite, 8 nm. thick, the component lamellae measuring 2.5 nm. (electron dense), 3 nm. (electron lucid), 2.5 nm. (electron dense). It delimits the protoplasm, including the pseudopodia.

Kavanau (1965) also suggested that the honeycombed membranes may have been constructed upon a template of a plasma-membrane in the open configuration. As we have found no indication of the site of honeycombed membrane formation we can make no comment on this suggestion.

Nucleus.—Nuclei are numerous, about 6 μ m in diameter, and distributed throughout the cytoplasm. The nuclear matrix is finely granular (Pl. 6, fig. A) and condensations of chromatin or heterochromatin have not been seen. There is a single nucleolus of the heterogenous type, usually with a central region of electron-dense granules, 20 nm. in diameter, and a peripheral ring of more tightly-packed smaller granules (Pl. 7, fig. A). A conventional nuclear membrane is present composed of

two tripartite membranes, each 6 nm. in width. Nuclear pores are numerous and made conspicuous by the presence of an electron-dense material which fills the pore (Pl. 6, fig. A). When cut in tangential section the pores of the nuclear membrane appear to have an electron-dense core 20 nm. in diameter, surrounded by a less dense ring 50 nm. in diameter, and then a dense margin 90 nm. in diameter (Pl. 7, fig. B). The closest centre to centre spacing observed is 100 nm., and there are approximately 13–15 pores per μm^2 . These figures are consistent with those given by Yoo & Bailey (1967) for nuclei from a variety of cells. Ribosomes are present on the cytoplasmic side of the outer nuclear membrane and in tangential section they are seen grouped as polysomes (Pl. 7, fig. B). Continuity between the outer nuclear membrane and the endoplasmic reticulum is common.

Endoplasmic reticulum and ribosomes.—Endoplasmic reticulum is not extensive in *Gromia* and usually occurs in regions free from cytoplasmic particles and organelles. The cisternae are distended and contain a material identical in appearance to the surrounding ground plasm (Pl. 9, fig. C). The cytoplasmic side of the endoplasmic reticulum membrane is studded with ribosomes, these are often grouped as polysomes which occur in crescents 8–12 ribosomes in length (Pl. 10, fig. B). Polysomes free in the ground plasm have not been found.

Mitochondria.—The mitochondria are usually spherical to ovoid, or, less commonly, elongate. They have protozoan-type tubular cristae which are occasionally seen to be continuous with the inner mitochondrial membrane.

Microbodies.—Microbodies are constant cytoplasmic organelles present in all specimens examined (Pl. 3, fig. A, Pl. 6, fig. A, Pl. 7, figs. C, D and E, Pl. 8, fig. B). We refer to these organelles as microbodies, because of their morphological resemblance to hepatic microbodies (Shnitka, 1966). The *Gromia* microbody in its typical form is spherical to ovoid, 0.5–1.0 μm in diameter, with a dense granular matrix and a single limiting membrane (Pl. 3, fig. A, Pl. 7, fig. C). In the matrix there are up to 4 tubular structures, or “nucleoids”, 30–35 nm. in diameter, with a wall thickness of 8 nm. The tubules when more than one is present lie approximately parallel to each other, the distance between each being variable. There is variation from this general pattern, especially in shape—some microbodies having an irregular outline (Pl. 8, fig. B). The density of the matrix is slightly variable (Pl. 7, fig. E), and occasionally the nucleoids vary from the simple tubular pattern (Pl. 7, fig. D). The variant nucleoids are ill-defined, slightly denser, regions of the matrix. Microbodies are found throughout the cytoplasm and are not spatially related to any particular part of the cytoplasm. The single limiting membrane is rarely resolved as a tripartite structure, but when resolved it varies from 6–6.5 nm. in thickness.

Similar microbodies are present in Foraminifera (Hedley *et al.*, 1967, and Hedley & Wakefield as a personal communication in, Hruban & Rechcigl, 1969, and unpublished observations). All Foraminifera so far examined (*Allogromia laticollaris*, *Allogromia* sp., *Boderia turneri*, *Cibicides lobatulus*, *Elphidium macellum*, *Iridia lucida*, *Rosalina leei* and *Shepherdella taeniformis*) are marine, intertidal or shallow-water forms, with the same habitat as *Gromia*, and all possess microbodies. Microbodies in Foraminifera differ from species to species, but within each species are morphologically constant. In *Boderia turneri* (Lagynidae) the microbodies have a simple nucleoid

consisting of 1-4 tubules, and are almost identical in morphology to *Gromia* microbodies. The only difference being that those of *Gromia* have a variable shape.

Recent biochemical studies on microbodies from rat liver and kidney have established the following enzymes as constituents of these organelles: catalase, D amino acid oxidase, L α hydroxy acid oxidase, uricase (liver only) and L amino acid oxidase (kidney only) (Baudhuin *et al.*, 1965). It has been suggested that these microbodies are important sites of hydrogen peroxide metabolism and they have been renamed peroxisomes (De Duve & Baudhuin, 1966). Peroxisomes are characterized by: (a) the presence of oxidases and catalase, these enzymes being linked in catalyzing the reduction of oxygen to water; and (b) morphologically as small discrete particles limited by a single membrane. Although *Gromia* and foraminiferan microbodies have a close morphological similarity to hepatic peroxisomes, the lack of any knowledge of their biochemistry precludes their inclusion as peroxisomes. In this context it is interesting to note that the above authors (Baudhuin *et al.*, 1965) recovered a particulate fraction from the protozoan *Tetrahymena pyriformis* which contained peroxisome enzymes.

Golgi apparatus.—Relatively large, well developed Golgi organelles, with a constant morphology are common throughout the cytoplasm (Pl. 8, fig. A). A branch of the endoplasmic reticulum is always present along the convex or proximal face (= forming face of Waley, 1966). The region between the endoplasmic reticulum and the first cisternae is occupied by many small vesicles, 30-100 nm. in diameter. The cisternae near the concave or distal face (= maturing face of Waley, 1966) are distended and contain small vesicles. The concavity formed by the curved cisternae is often occupied by a large vacuole containing vesicles and a poorly-defined fibrillar material (Pl. 8, fig. A). Similar vacuoles are present elsewhere in the cytoplasm, where they are not associated with a Golgi apparatus (Pl. 8, fig. D). Some of these vacuoles are seen to be adjacent to (Pl. 8, fig. C) and in continuity with the plasma-membrane, their contents being in contact with the fibrillar material of the shell (Pl. 9, fig. A). It is tempting to suggest that these vacuoles, in three different positions, at the plasma-membrane, free in the cytoplasm, and closely associated with the Golgi apparatus, represent stages in a continuous process. The two end points in this process are the Golgi apparatus and the plasma-membrane. The vacuoles are formed either at the plasma-membrane, move into the cytoplasm and become associated with the Golgi apparatus, or, are formed at the Golgi apparatus move through the cytoplasm and fuse with the plasma-membrane. The direction of movement is not known. A brief consideration of other cells, where some of the functions of the Golgi apparatus are reasonably well established, may be useful here. In Brunner's gland of the mouse (Friend, 1965), goblet-cells of the rat colon (Neutra & Leblond, 1966), and wheat seedlings (Northcote & Pickett-Heaps, 1966) one of the known functions of the Golgi apparatus is the synthesis of polysaccharide, which is subsequently exported from the cell. A function of the Golgi apparatus in exocrine pancreatic cells of the guinea-pig is to concentrate enzyme, and enzyme precursors, into zymogen granules which are also exported (Caro & Palade, 1964, and Jameson & Palade, 1967). In rat transitional epithelium the Golgi apparatus produces a specialized thickened plasma-membrane (Hicks, 1966). The particular function of

the Golgi apparatus in a particular cell will be dependent on the function of that cell, but as the above examples indicate these fit into a generalized pattern of secretion, carbohydrate synthesis and subsequent export from the cell. This evidence from other cells suggests a direction of movement for the vacuoles in *Gromia* i.e. from Golgi apparatus to plasma-membrane. The opposite direction has been suggested to occur in amoeba (Daniels, 1964), but subsequent studies, using alcian blue as label, indicate that the endocytic vacuoles become food-vacuoles and do not contribute to the Golgi apparatus (Hayward, 1963, Chapman-Andreson & Nilsson, 1967). Assuming a direction of movement of vacuoles from Golgi apparatus to plasma-membrane the details of the process in *Gromia* are probably as follows: Protein together with polysaccharide precursor is budded off from the endoplasmic reticulum in vesicles around the proximal face of the Golgi apparatus. These vesicles coalesce and form the proximal cisternae. The polysaccharide precursors are polymerized into polysaccharide which with protein is organized into wall building units. As this takes place the cisternae move across the Golgi stack as other cisternae leave the distal face and more are formed at the proximal face. Near the distal face, the cisternae dilate forming vacuoles. These are released into the cytoplasm, migrate to the plasma-membrane, fuse with the plasma-membrane, and discharge their contents.

A feature of this process worthy of discussion is the variation in membrane morphology of the various components. The membranes of the vacuoles and contained vesicles are 8 nm. in width, tripartite and not heavily stained— β cytomembranes (Sjostrand, 1967). The membranes of the endoplasmic reticulum and Golgi apparatus are 6.5 nm. in width, electron dense and rarely resolved as tripartite— α and γ cytomembranes (Sjostrand, 1967). These membranes are structurally distinct (Sjostrand, 1963a, b, c), the α and γ cytomembranes having a globular substructure, and the β cytomembranes having a laminar substructure, and it has been suggested that transformation from one type to another does not occur (Ledbetter, 1962). A similar membrane change occurs in those instances cited above. For example, zymogen granules, transitional epithelium membrane and the vacuoles in the cells of Brunner's gland all have β cytomembranes and all originate from the Golgi apparatus— γ cytomembranes. Membrane variation within the Golgi apparatus has been described by Grove *et al.* (1968)—the membranes of the proximal cisternae are lightly stained and not resolved as tripartite, those of the distal face are densely stained and clearly tripartite, and the intercalary cisternae vary between these two extremes. From these examples it appears that transformation from γ cytomembranes to β cytomembranes is possible.

Secretion granules.—In the peripheral cytoplasm and in the cytoplasm around the oral region there are bodies not seen elsewhere in the cytoplasm, and which we shall refer to as "secretion granules". They are spindle shaped 2–3 μm in length, 1–1.5 μm in width, limited by a single membrane and possess a dense granular matrix differentiated into two regions (Pl. 9, fig. B and D, Pl. 10, fig. A). One of these regions is in the form of a rod, 0.2 μm in width, and extends the length of the granule. (Pl. 9, fig. B, Pl. 10, fig. A). The second region is composed of electron-dense granules, 8–10 nm. in diameter, tightly packed and arranged in concentric layers (Pl. 10, fig. A). The third region is an electron-dense reticular body composed of

small granules 10–15 nm. in diameter (Pl. 9, fig. D). Although nothing is known about these granules beyond their morphology, two observations indicate their possible function. Firstly, the contents of the granules often appear to have contracted away from the limiting membrane, giving the granule the appearance of a vacuole-contained body. Secondly, many of the granules have lost most of their internal contents, apart from the granular regions, which appear to be breaking down to produce a fibrillar material (Pl. 10, fig. C and D). We consider it likely that this is the fibrillar mucous material which eventually lines the pseudopodia.

Xanthosomes and stercomata.—Xanthosomes and stercomata are hard brittle granules composed of concreted waste—material and are present throughout the cytoplasm (Pl. 6, fig. A). They have been discussed in a previous publication (Hedley & Bertaud, 1962) to which nothing new can be added at present.

Pseudopodia.—A lucid description of the pseudopodia and their activity in living *Gromia* is given by Jepps (1926): "The pseudopodia are perfectly hyaline during life, no granules being visible in them even under an oil immersion lens. They emerge very slowly, as a little bunch of stiff slender spikes, from an area of the cytoplasm lying just inside the mouth of the shell and free from ingesta. They extend in all directions, gently waving about as if in search of something of which to take hold. When a pseudopodium comes up against a solid object it sticks to it and flows out over it. As the pseudopodia increase in size they branch, and become irregularly varicose and ridged so that they look somewhat like the gnarled roots of a tree. From swollen places or knots there arise fresh pseudopodia extending at wide angles and often anastomosing with others in the vicinity. Some may creep back over the surface of the shell: otherwise there is no extramural protoplasmic layer." It must be emphasized that movement of the pseudopodia is extremely slow and especially so when compared with that encountered in Foraminifera. Movement is of two types, first, of a pseudopodium as a whole, and secondly, of protoplasm within a pseudopodium. Once an animal has begun to extrude pseudopodia at least 20 minutes is required for their full extension (Pl. 1). When fully extended, movement of a pseudopodium as a whole is rare. Movement of protoplasm along an extended pseudopodium has not been seen, although specimens have been examined using bright field, phase contrast, interference and polarizing microscopy.

For fine structure studies pseudopodia were fixed in a variety of fixatives (see Material and Methods) in each of the following conditions: (i) whilst being extruded; (ii) when fully extended; and (iii) when contracting, due to release of the animal from the substrate. In each case the fine structure of the pseudopodia was the same, consisting of ground-plasm, limited by a membrane, and surrounded by mucus (Pl. 10, fig. E). At higher magnification (Pl. 11, fig. A), the membrane is seen to be tripartite, 9.5 nm. in width, and the ground-plasm amorphous. The only formed elements within the pseudopodia are rare vesicles and dense bodies of unknown nature and function (Pl. 11, fig. C). The mucous layer, approximately 1 μ m thick, is fibrillar with the fibrils parallel to the length of the pseudopodium (Pl. 11, fig. C).

There is no discernable difference in fine structure along the length of the pseudopodia from the oral capsule to the distal extremities. On the cytoplasmic side of the oral capsule however, the ground-plasm of the pseudopodia is more condensed. The

pseudopodia arise from the cytoplasm in this region at approximately 100–200 μm from the oral opening. The junction of the pseudopodia with the cytoplasm is very sharp (Pl. 11, fig. D, Pl. 12, fig. A). and there is no discernable structure associated with this abrupt change. The mucous lining to the pseudopodia is present in this region (Pl. 12, fig. A) and most likely originates from mucus-containing vesicles, which are concentrated in the oral cytoplasm (Pl. 12, fig. A). Where these originate is not known, although there are indications that the "secretion granules" may break down to liberate the mucus (Pl. 10, fig. C and D). Such granules are present in large numbers in the oral region.

It is useful to compare the pseudopodia of *Gromia* with recent accounts of pseudopodia in Foraminifera (Wolfarth-Botterman, 1961, Hedley *et al.*, 1967) and Testacea (Berrend, 1964, Wohlman & Allen, 1968). The enigmatic nature and taxonomic significance of the pseudopodia of *Gromia* have been discussed briefly (Hedley, 1964). The pseudopodia of Foraminifera are, at the optical microscope level, similar throughout the group. They form a complex anastomosing network of rapidly moving pseudopodia with each strand supporting two streams of oppositely directed granular protoplasm moving at about 8–15 μm per second (Allen, 1964). Electron microscopy of the pseudopodia has shown that mitochondria, vesicles (Wolfarth-Botterman, 1961, and Hedley *et al.*, 1967) and microtubules (Hedley *et al.*, 1967, and unpublished observations) are present. The microtubules may be few or may fill the cross section of a pseudopodium, and, unlike those in Heliozoa (Tilney *et al.*, 1966), have a random arrangement. This is very different from *Gromia* whose pseudopodia move extremely slowly, have no granules, have no perceptible movement within the pseudopodia, and whose fine structure is characterized by an absence of any formed elements.

Microtubules are labile cell constituents (Porter, 1966), and their absence in *Gromia* pseudopodia could be due to any of the following reasons: (i) they were lost on fixation; (ii) they were not present in that part of the pseudopodium examined, at the time of fixation, but may have been present at some earlier time when the functional state of that part of the pseudopodium was different; or (iii) they are not normal constituents of the pseudopodia. It is doubtful if the absence of microtubules is due to the first two reasons, as the fixation procedures used usually preserve microtubules, and the pseudopodia were fixed in three functional states—extending, fully extended and retracting. Many sections of each were examined and microtubules were not demonstrated. It would appear that microtubules are not normal constituents of pseudopodia in *Gromia*.

Microtubules are usually considered to have a cytoskeletal function, and are common constituents of fine cellular extensions (Porter, 1966). Their absence in *Gromia* pseudopodia indicate that the rigidity of these structures is due to other unknown factors. Cytoplasmic streaming has not been observed in *Gromia* pseudopodia, and filaments approximately 5 nm. in diameter, commonly found in streaming cytoplasm (Nachmias, 1968, Wolpert *et al.*, 1966), and often considered as providing the force for cytoplasmic streaming (Wolpert, 1962), have not been detected.

The Testacea are a more diverse group than the Foraminifera, there are two main types of pseudopodia within the group, lobopodia and filopodia. In *Diffugia*

(Testacealobosia, De Saedeleer, 1934) there are usually 1-4 lobopodia with small side-branches. Pseudopodial movement is rapid and granular streaming is present within the pseudopodia, the speed of movement ranges from 2 μm to at least 15 μm per second (Wohlman & Allen, 1968). The fine structure of the pseudopodia includes vesicles, electron-dense granules and extensive tracts of microfilaments (Wohlman & Allen, 1968). In *Cyphoderia* (Testaceaifilosa) there are usually 5-6 filopodia with small side-branches, pseudopodial movement is rapid, and the speed of movement of protoplasm within the pseudopodia is about 4-5 μm per second (Berrend, 1964). The two types of testacean pseudopodia are quite different from *Gromia* pseudopodia.

GAMETES

The main observations of earlier biologists concerning gametogenesis and syngamy (Wright, 1861; Schaudinn, 1894, 1899; Zarnik, 1907; Awerinzew, 1910; Lwoff, 1925) have been reviewed by Jepps (1926). She was the first worker to describe nuclear division and the flagellated gametes. Further illustrations of gametes have been given by Le Calvez (1938) and Hedley (1962). Arnold (1966) reported the pairing of adults with the production of isogametes, and has proposed a tentative life-cycle.

Gametes have a single mucronate flagellum, 10 μm in length (Pl. 12, fig. B and C), with no appendages. This is only half the length of the flagellum described from optical microscopy (Jepps, 1926).

Although the fixation of gametes for fine structure studies was poor and the micrographs are mostly unfit for publication they have been useful in determining the internal organization of the gametes (Text-fig. 4). The body of a gamete is 2-3 μm in diameter, roughly spherical and limited by a plasma-membrane with no outer coating or wall. The single nucleus, 1.5 μm in diameter, contains dense chromatin with a few irregularly-shaped less-dense regions. There are usually two mitochondria, several fat droplets, and a small poorly-defined body which may be a microbody. There is a single flagellum and two basal bodies arranged at right angles. Each flagellum contains nine pairs of peripheral and one pair of central tubules. The presence of a single flagellum and two basal bodies is usually thought to be due to the loss of a flagellum during phylogeny from an organism originally having two flagellae (Manton, 1965). Such reduction has occurred sporadically in flagellate plant-cells (Manton, 1965). The arrangement of the fibres in the tips of mucronate flagellae is not known (Manton, 1965). In *Gromia* it appears that the outer ring of fibres stops at the junction of the tip, and only the central pair continue into the tip (Pl. 11, fig. B). This arrangement is similar to that of *Micromonas pusilla*, which has a long hair point (Manton, 1959).

There are two regular and obvious components of gamete cytoplasm whose nature and function are unknown, neither of which has been seen in adult animals. The first is a spherical to ovoid structure, 1 μm in diameter, limited by a single membrane, and containing two types of ill defined structures (Pl. 12, fig. D, Text-fig. 4-X). The second structure is membraneous and its morphology poorly understood (Pl. 12, fig. E, Text-fig. 4-Y).

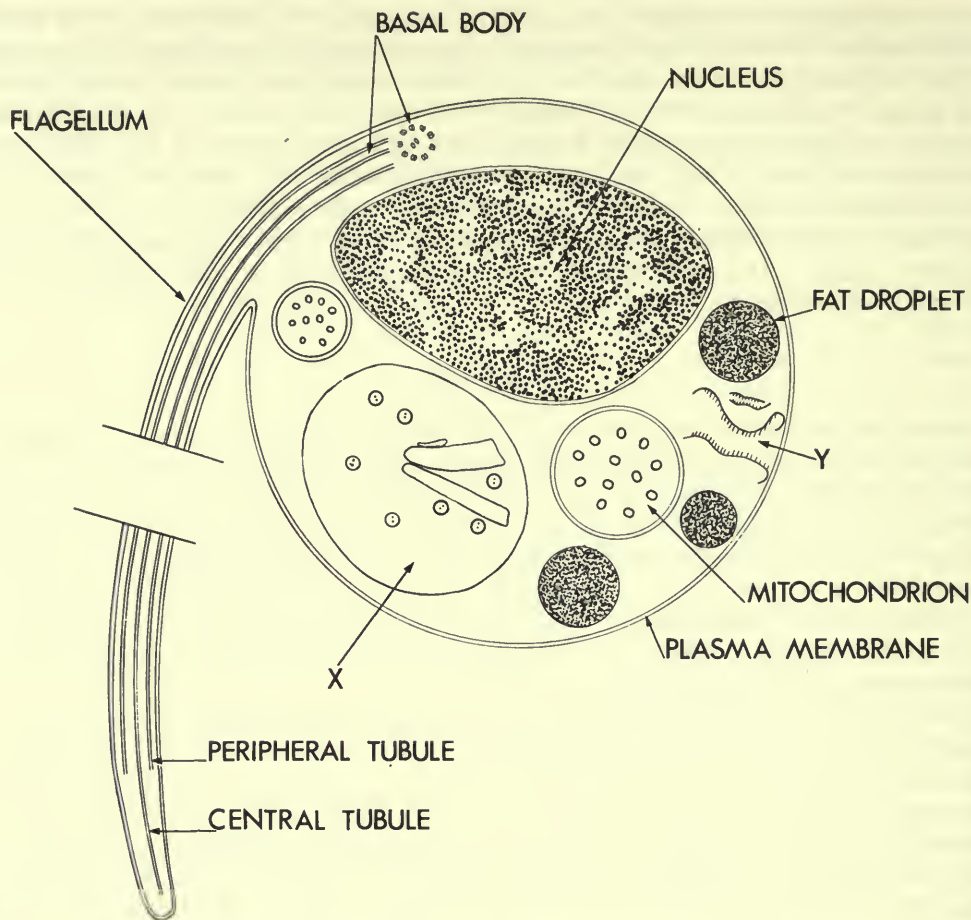


FIG. 4. Diagram of a gamete based on the examination of several micrographs. X, body of unknown function containing block-shaped and oval structures; Y, membranous structure of unknown function. Both X and Y constituents are noted in the text

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PLATE I

An adult *Gromia oviformis* Dujardin, 1839, with pseudopodia extended. $\times 30$.



PLATE 2

FIG. A. Cross section through the shell and peripheral cytoplasm: EDL, electron-dense layer; OW, outer wall; HM, honeycombed membranes; F, fibrillar material; PM, plasma-membrane; C, cytoplasm. $\times 46,000$.

FIG. B. Section of an outer wall canal illustrating the concentric arrangement of fibres. $\times 93,000$.

FIG. C. Section through a wall canal: EDL, electron-dense layer; the arrow indicates concentration of electron dense spots referred to in the text. $\times 36,500$.

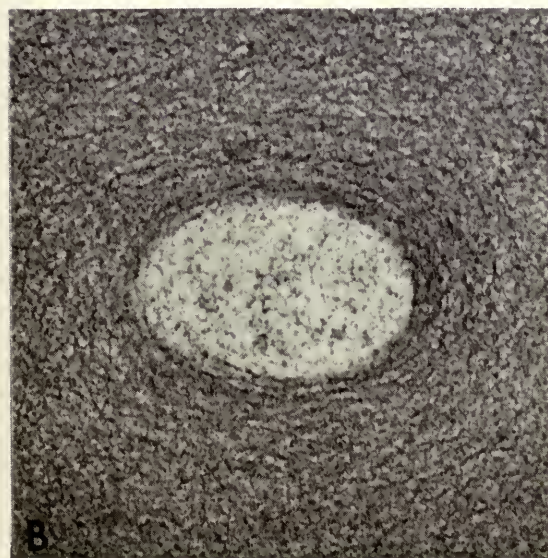
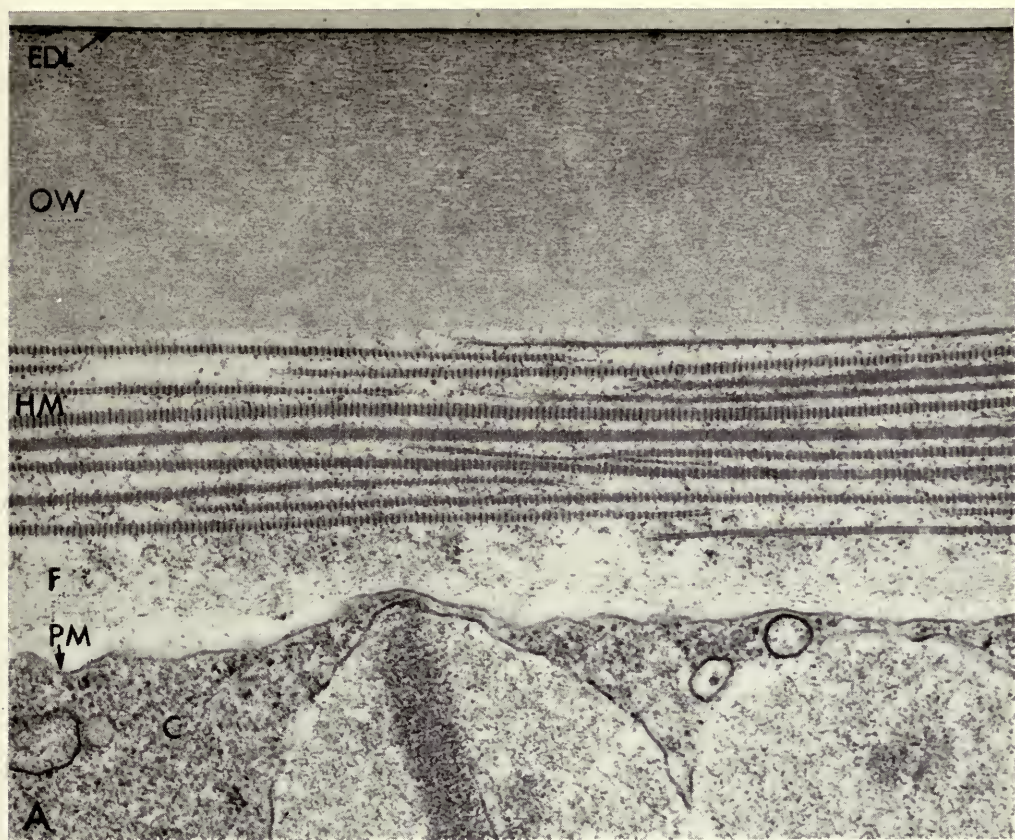


PLATE 3

FIG. A. Cross section through the shell and peripheral cytoplasm: EDL, electron-dense layer; OW, outer wall; HM, honeycombed membranes—T₁ = type 1, T₂ = type 2, T₄ = type 4; F, fibrillar material; PM, plasma-membrane; MB, microbody. $\times 57,000$.

FIG. B. Cross section through the outer wall: EDL, electron-dense layer; P, pore. $\times 86,000$.

FIG. C. A tangential section in which two honeycombed membranes have produced a Moiré effect. $\times 90,500$.

FIG. D. Section through a canal pore (P). $\times 90,000$.

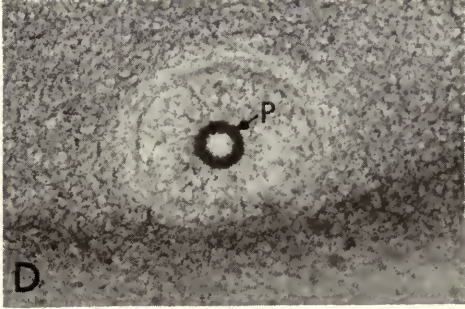
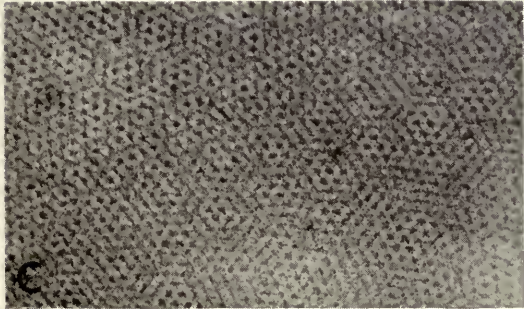
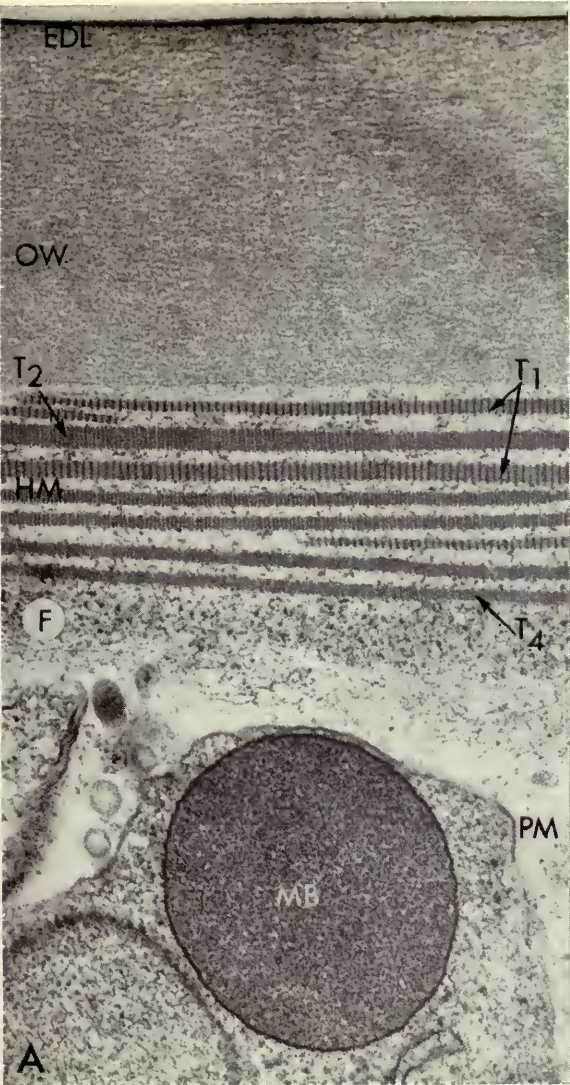


PLATE 4

FIG. A. Tangential section of a honeycombed membrane. $\times 121,000$.

FIG. B. Cross section of honeycombed membranes: T₁ = type 1, T₃ = type 3. $\times 47,000$.

FIG. C. Oblique section of a honeycombed membrane. At "A" the membrane is sectioned tangentially, at "B" it is sectioned nearly vertically. $\times 81,500$.

FIG. D. Section through the microtubules of the oral capsule: M, microtubules; L, fibrils; LL, fibrillar layer. $\times 90,500$.

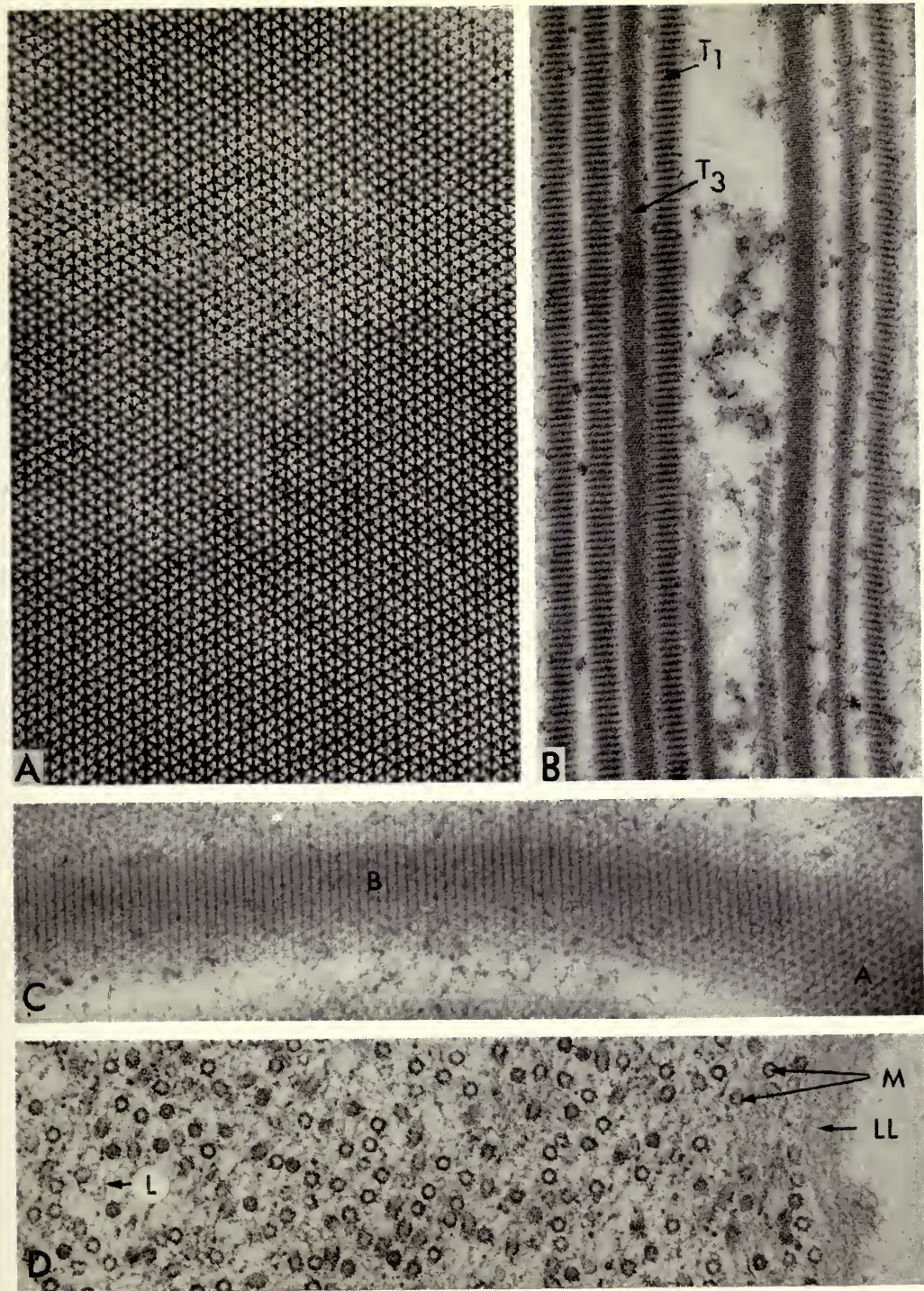


PLATE 5

Cross section through the oral capsule (as in text-fig. 3): EDL, electron-dense layer; OW, outer wall; OW 1, outer extension of the outer wall; OW 2, inner extension of the outer wall; OW 3, thickening of the outer wall material at the junction; HM, honeycombed membranes; F, fibrillar material; PM, plasma-membrane; C, cytoplasm; M, microtubules; L, fibrils of the oral capsule. $\times 12,500$.



PLATE 6

FIG. A. General view of the cytoplasm: N, nucleus; NP, nuclear pore; MB, microbody; MT, mitochondria; S, stercomata; X, xanthosomes. $\times 13,000$.

FIG. B. Section of the oral capsule stained with silver methenamine: EDL, electron-dense layer; OW, outer wall; M, microtubular mass—positive staining for polysaccharide. $\times 20,000$.

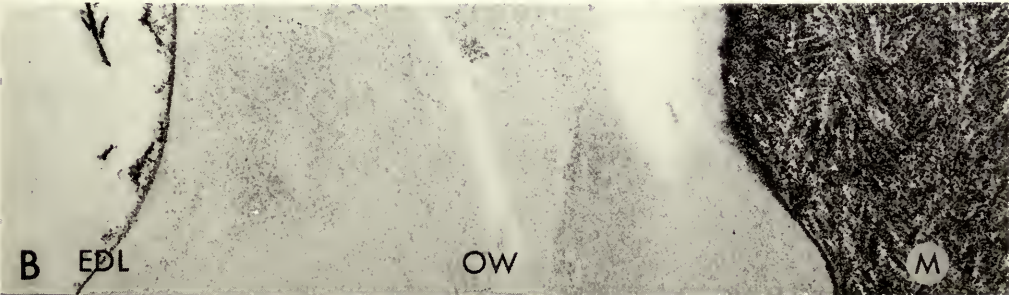
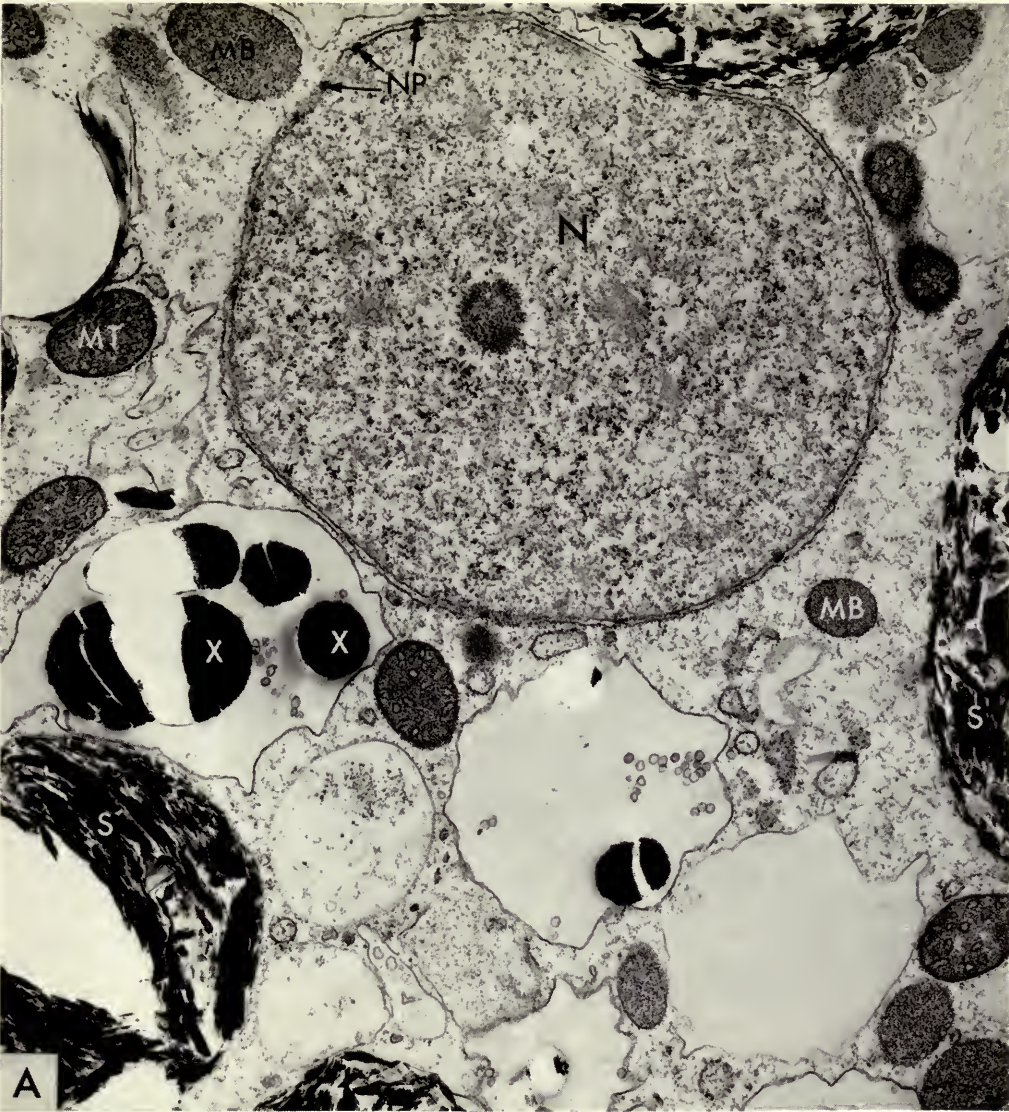


PLATE 7

FIG. A. Part of a nucleus containing a nucleolus which is composed of two regions, G 1 finely granular and G 2, coarsely granular. $\times 8,500$.

FIG. B. A tangential section of a nuclear membrane containing several nuclear pores, NP; P, polysomes. $\times 49,500$.

FIG. C. A microbody with a single limiting membrane, dense granular matrix and a single tubule T. $\times 75,500$.

FIG. D. A microbody containing two tubules T, and a variant nucleoid H. $\times 57,000$.

FIG. E. Three adjacent microbodies showing variation in matrix density. $\times 36,000$.

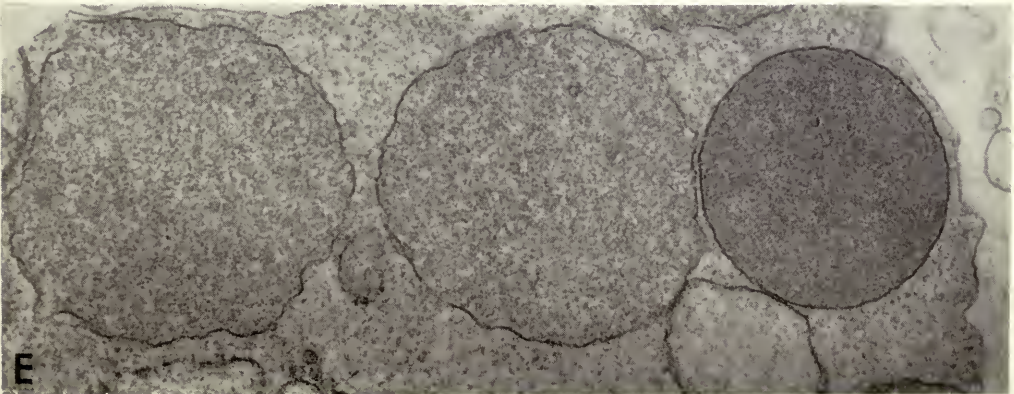
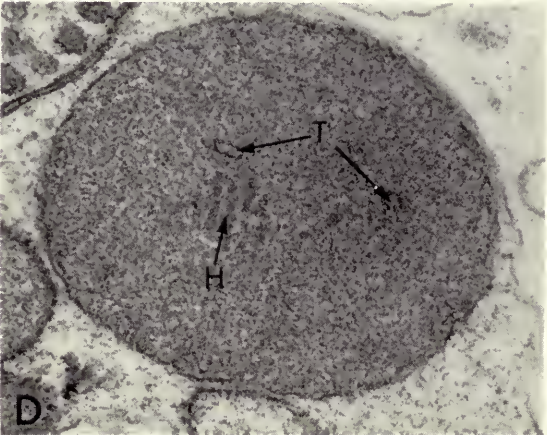
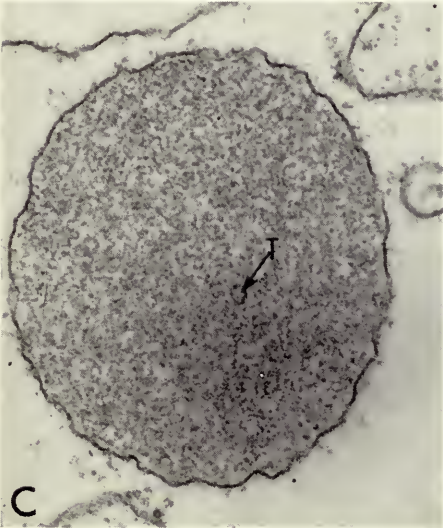
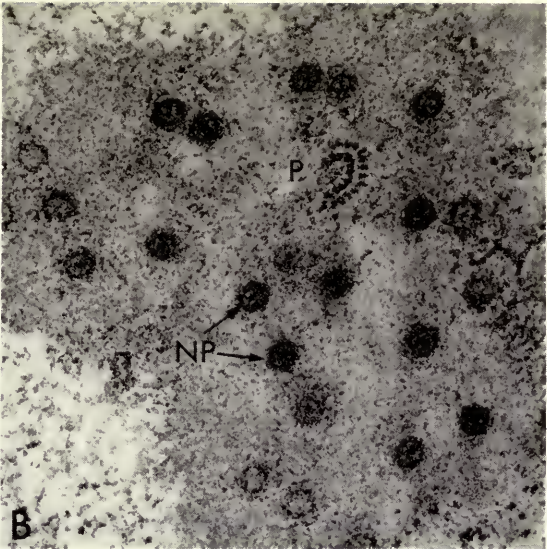
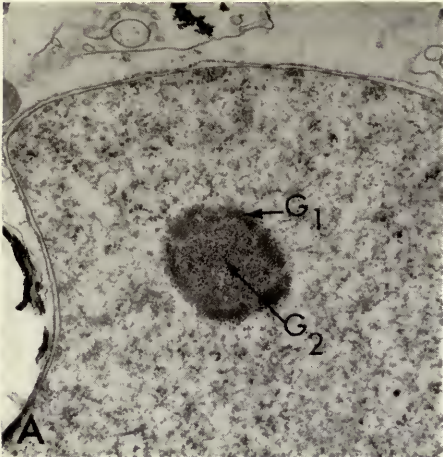


PLATE 8

FIG. A. Golgi apparatus: ER, endoplasmic reticulum; V, vesicle; VO, vacuole containing fibrillar material and vesicles. $\times 55,000$.

FIG. B. Microbody with irregular outline: T, tubules. $\times 60,000$.

FIG. C. VO, vacuole containing fibrillar material and vesicles near the plasma-membrane, PM; HM, honeycombed membranes. $\times 60,000$.

FIG. D. Vacuole containing fibrillar material and vesicles, free in the cytoplasm. $\times 59,000$.

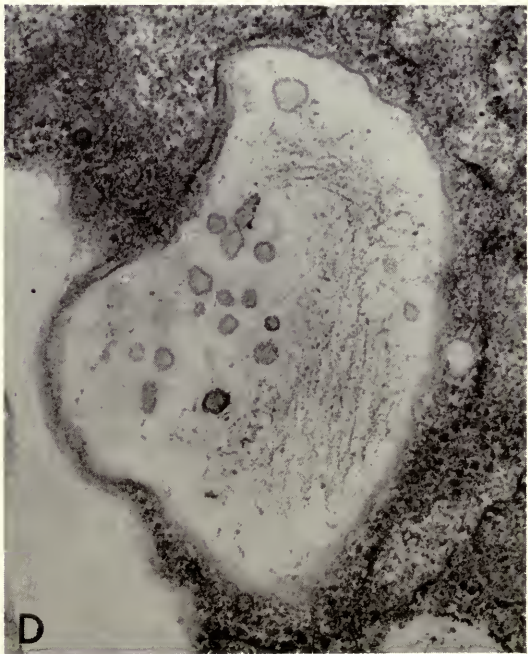
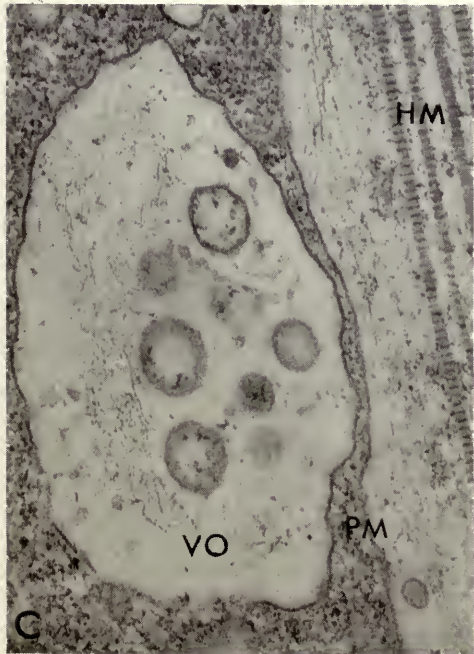
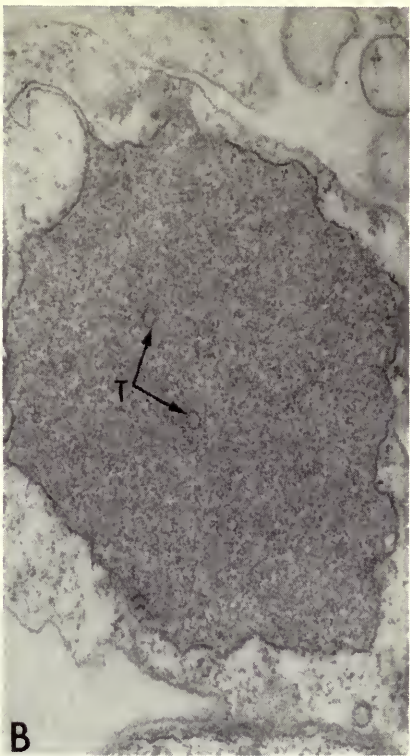


PLATE 9

FIG. A. Vacuole in continuity with the plasma-membrane, discharging its content of fibrillar material and vesicles: F, fibrillar material of the wall. $\times 60,500$.

FIG. B. Secretion granule. $\times 35,000$.

FIG. C. Section showing the distended cisternae of the endoplasmic reticulum. Note that the contents of the cisternae appear identical to the ground plasm. $\times 53,000$.

FIG. D. Secretion granule with a differentiated region. $\times 26,500$.

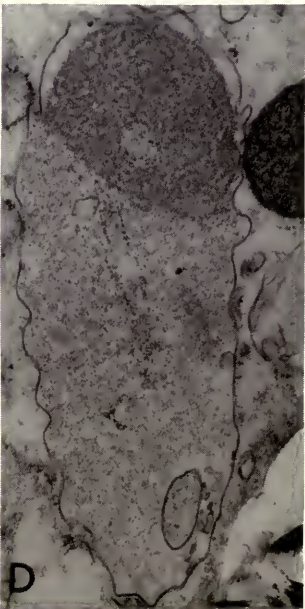
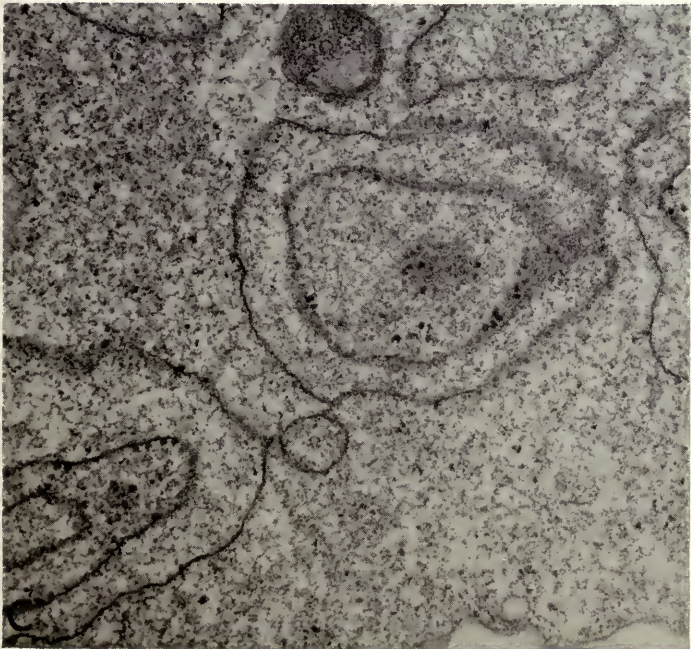
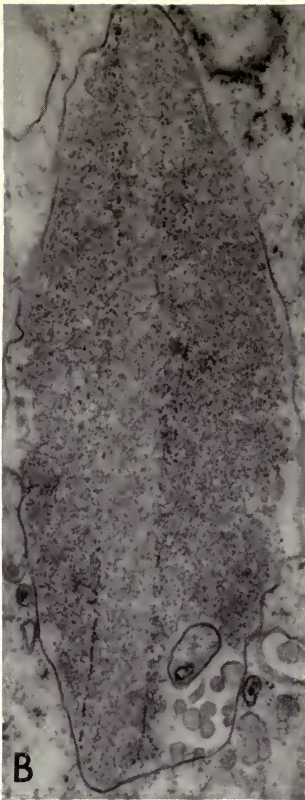
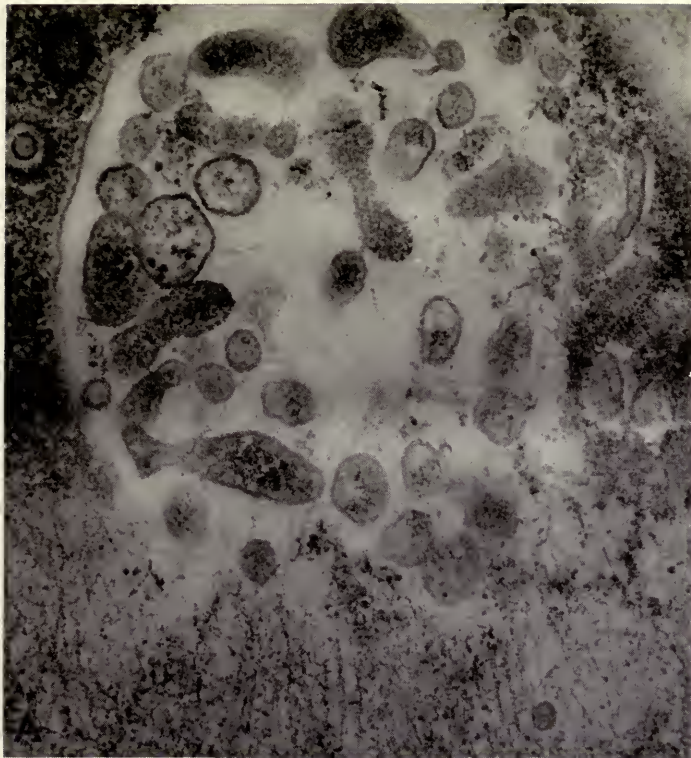


PLATE 10

FIG. A. Two secretion granules, one with a central differentiated region. $\times 46,500$.

FIG. B. Tangential section of part of the endoplasmic reticulum, ER; with polysomes, P.
 $\times 96,500$.

FIGS. C, D. Secretion granules breaking down to form fibrillar material. $\times 34,000$.

FIG. E. Part of a pseudopodium: M, surrounding mucus; PM, plasma-membrane; G, ground-plasm. $\times 12,500$.

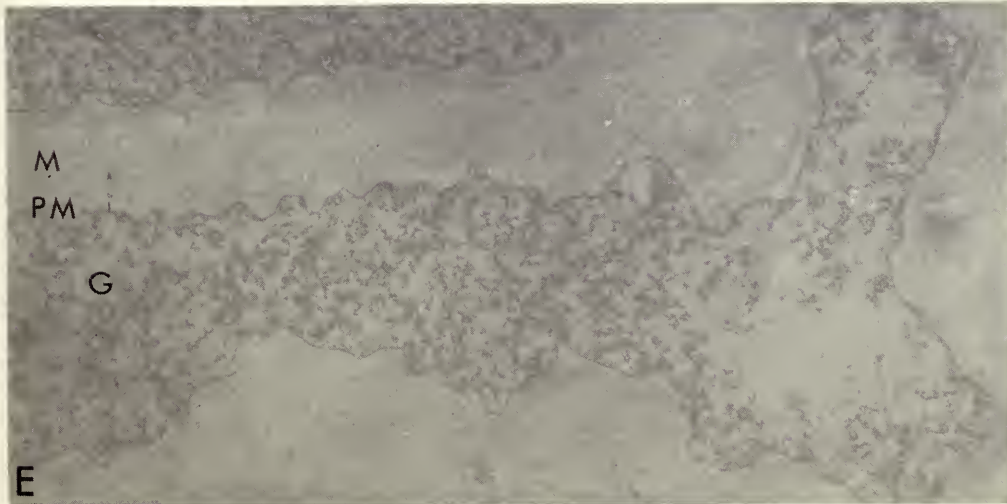
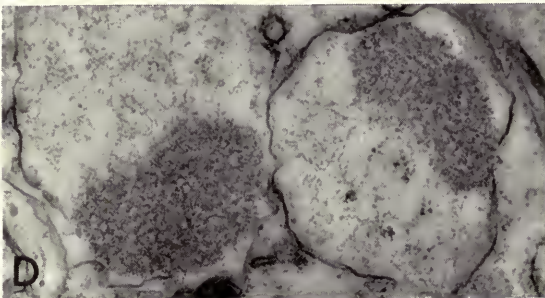
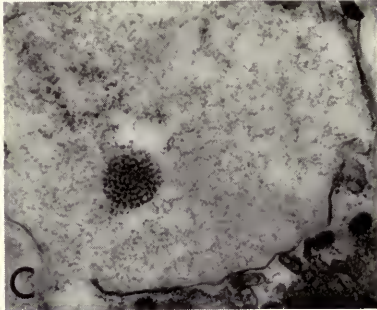
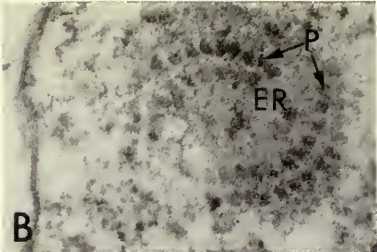
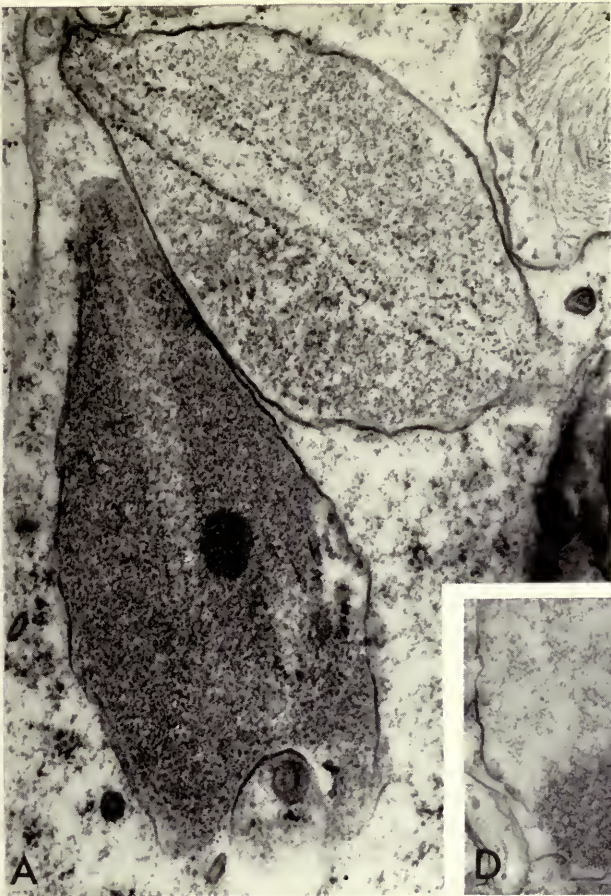


PLATE II

FIG. A. Part of a pseudopodium: M, mucous layer; PM, plasma-membrane; G, ground-plasm. $\times 55,000$.

FIG. B. Section through the tip of a gamete flagellum: PM, plasma-membrane; PT, peripheral tubules; CT, central tubules. $\times 75,000$.

FIG. C. Part of a pseudopodium: M, mucous layer; PM, plasma-membrane; V, vesicles; DB, dense body. $\times 25,000$.

FIG. D. Junction of a pseudopodium and cytoplasm: PG, pseudopodial ground-plasm; C, cytoplasm; V, vesicles containing mucus. $\times 12,000$.

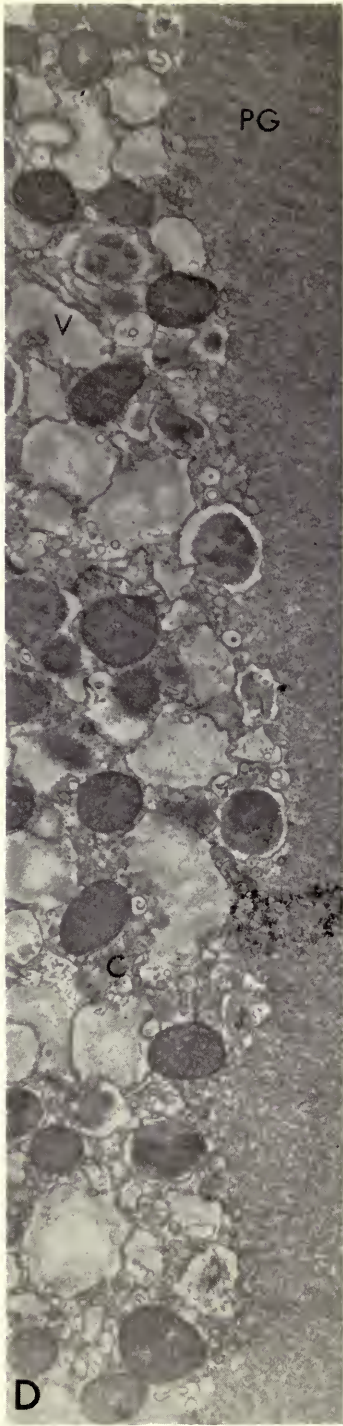
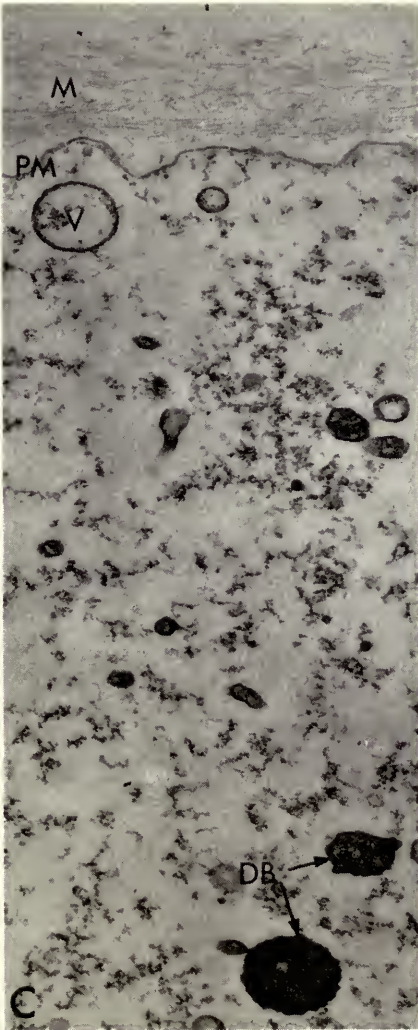
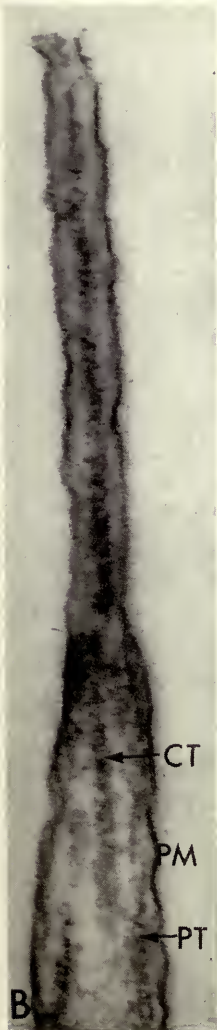
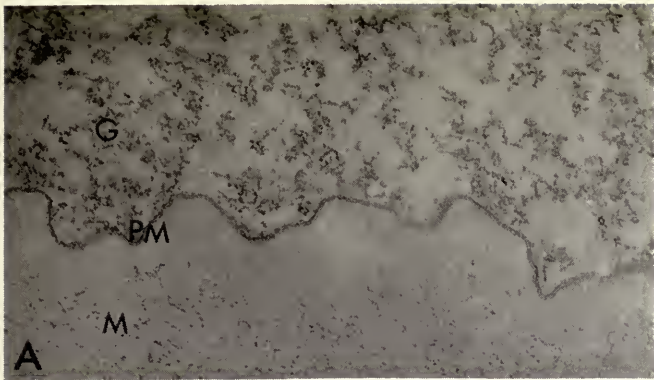


PLATE 12

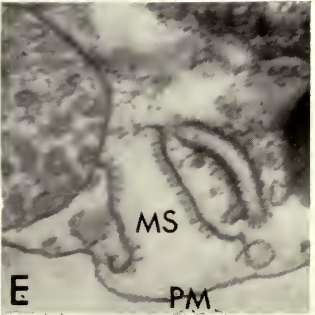
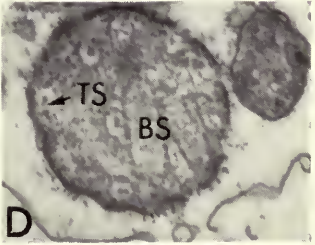
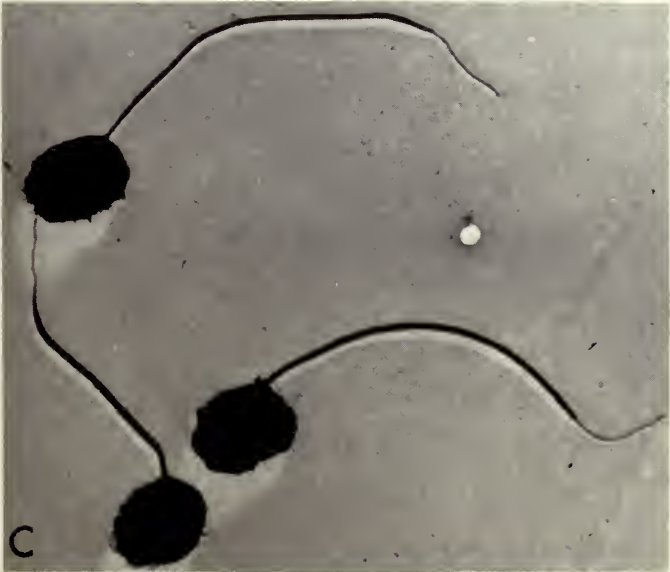
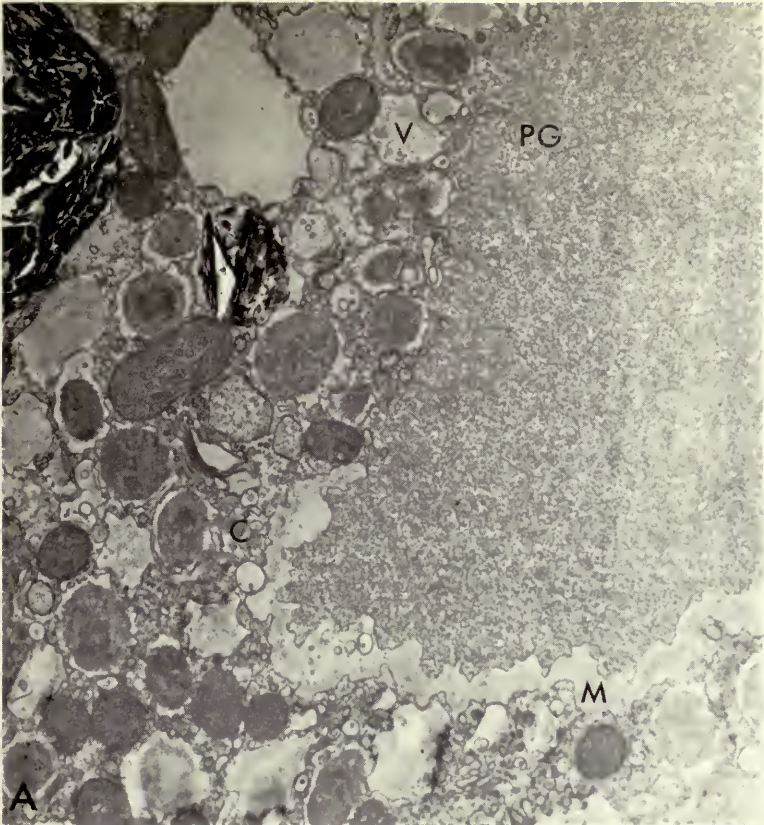
FIG. A. Junction of a pseudopodium and cytoplasm: PG, pseudopodial ground-plasm; C, cytoplasm; V, vesicles containing mucus; M, mucous layer separating the pseudopodium from cytoplasm. $\times 12,000$.

FIG. B. Shadowed preparation of a gamete. $\times 7,000$.

FIG. C. Shadowed preparation of gametes. $\times 6,000$.

FIG. D. Enigmatic body present in gametes: BS, block-like structure; TS, tubular structure. $\times 28,000$.

FIG. E. MS, membraneous structure present in gametes; PM, plasma-membrane. $\times 37,000$.



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(ACARI CRYPTOSTIGMATA)
FROM NORTH BORNEO



G. W. RAMSAY
&
J. G. SHEALS

BULLETIN OF
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ZOOLOGY

Vol. 18 No. 3

LONDON: 1969

EUPHTHIRACAROID MITES
(ACARI, CRYPTOSTIGMATA)
FROM NORTH BORNEO

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EUPHTHIRACAROID MITES (ACARI, CRYPTOSTIGMATA) FROM NORTH BORNEO

By G. W. RAMSAY¹ & J. G. SHEALS

THE results of a preliminary numerical taxonomic survey of the Euptyctima (Sheals, in press) called into question the validity of several generic concepts. In particular, amongst the Euphthiracaroida, the analyses showed that an undescribed species from North Borneo (unit 4 of the study), whilst having features currently regarded as being characteristic of the genus *Austrotrititia* Sellnick, really merited the status of a separate genus, which, moreover, on a greatest attribute basis, would be rather isolated phenetically. No formal proposals for new taxa were made in this study and the material was obtained by sampling unsorted collections from geographically widely separated areas, including a series of Berlese funnel extracts of soil and litter presented to the British Museum (Natural History) by the Royal Society North Borneo Expeditions 1961 and 1964.

A formal description of "unit 4" was clearly necessary but the apparently unusual combination of attributes found in this species suggested that the Borneo euphthiracaroid fauna might be worthy of further study and prompted a more detailed examination of the material collected by these expeditions. In addition to "unit 4" the samples were found to contain representatives of a second undescribed genus, an undescribed species referable to the genus *Austrotrititia* Sellnick and a new subspecies of *Microtrititia tropica* Märkel. These mites were found in three series of samples with data as follows:

- 1961 Expedition B74: Kundazan. Site on mid-slope of easterly facing hillside. Primary Forest. Elevation approximately 1,402 m (given as approximately 4,600 ft.). Soil a deep acid yellow earth with thick mor humus layer. pH of litter (field determination), 3.2.
- 1964 Expedition B124: Pinosuk Plateau, site near R. Mesilau, Kinabalu region. Elevation approximately 1,615 m (given as approximately 5,300 ft.). Humus podzol: "old" soil on mixed drift of granodiorite and shale.
- 1964 Expedition B161: Elevation approximately 1,646 m (given as approximately 5,400 ft.). Other data as for B124.

We are indebted to Mr. G. P. Askew, the expedition's pedologist, for collecting the samples and for extracting the animals under difficult field conditions.

¹Nuffield Commonwealth Travelling Fellow.

ORIBOTRITIIDAE Grandjean 1954

The family diagnosis given by Grandjean (1967) can be paraphrased as follows:

The anal plates, which lack an anterior triangular zone containing interdigitating lobes, are generally discrete and delimited on their antiaxial border by a cleft which separates them from the ventral shield. Fusion of the anal and ventral shields, with or without a suture line, may occur, but only posteriorly up to approximately the level of seta *an*₂. The genital plates may be delimited antiaxially by a complete or incomplete suture or they may be completely fused with the ventral shield. The ventral shield on each side may be entire or incompletely divided by an oblique transverse asclerotized line (*trv*) which is a continuation of the ano-genital junction. One or two exobothridial setae are present and the number of palp segments varies from three to five. A lateral abdominal gland is present. The bothridia have no tracheoles or brachytracheae. The animals lay prelarvae which are coloured and which have a strongly sculptured integument.

Grandjean's concept of the family must now be slightly modified since bothridial tracheoles have been observed in *Terratritia askewi*, a new oribotritiid described below.

Terratritia askewi gen. et sp. nov.

The five specimens available for study were pale brown in colour with the rims of the notogaster reddish brown.

Aspis (Text-figs. 3 and 4): 325–400 μm long, 220–280 μm wide and with a greatest depth of about 140 μm , moderately broad and slightly rounded laterally. The integument is generally finely porose but over the rostral area (which is slightly paler) it is striated and sparsely punctated. A single sharp lateral carina is present starting rather far forward at a point anterior to setae *la*. A posterior median apodeme ("scheitelbalken" of Märkel, 1964) is present and a small bothridial scale lies behind but at the same level as the sensillus. A weak transverse line of striations is present at the level of the bothridia. The arrangement of the setae on the aspis is somewhat reminiscent of *Perutritia* and *Mesotritia*, with the interlamellar setae (*il*) inserted close to the bothridia near the lateral margin. The rostral setae (*ro*) are procumbent, smooth and fine and reach beyond the anterior margin of the rostrum. The lamellar setae (*la*) are also procumbent but much shorter than the rostrals. The interlamellar setae (*il*) are fine, smooth and erect and longer than the lamellars. The bothridium (Text-fig. 12) has a large smooth outer chamber and a smaller inner chamber with many annulations. Approximately five short finger-like processes arise from the outer chamber. Additionally there are approximately four tracheoles although these were not visible in every specimen. The sensillus is long, smooth and tapering and there are two pairs of exobothridial setae (*ex*₁, *ex*₂).

Notogaster (Text-figs. 1 and 2): Diagonal length 575–800 μm , with a greatest depth of 375–520 μm and a greatest width of 375–480 μm , elongated and pointed posteriorly. The integument is finely porose and weakly tuberculate with relatively large refrac-

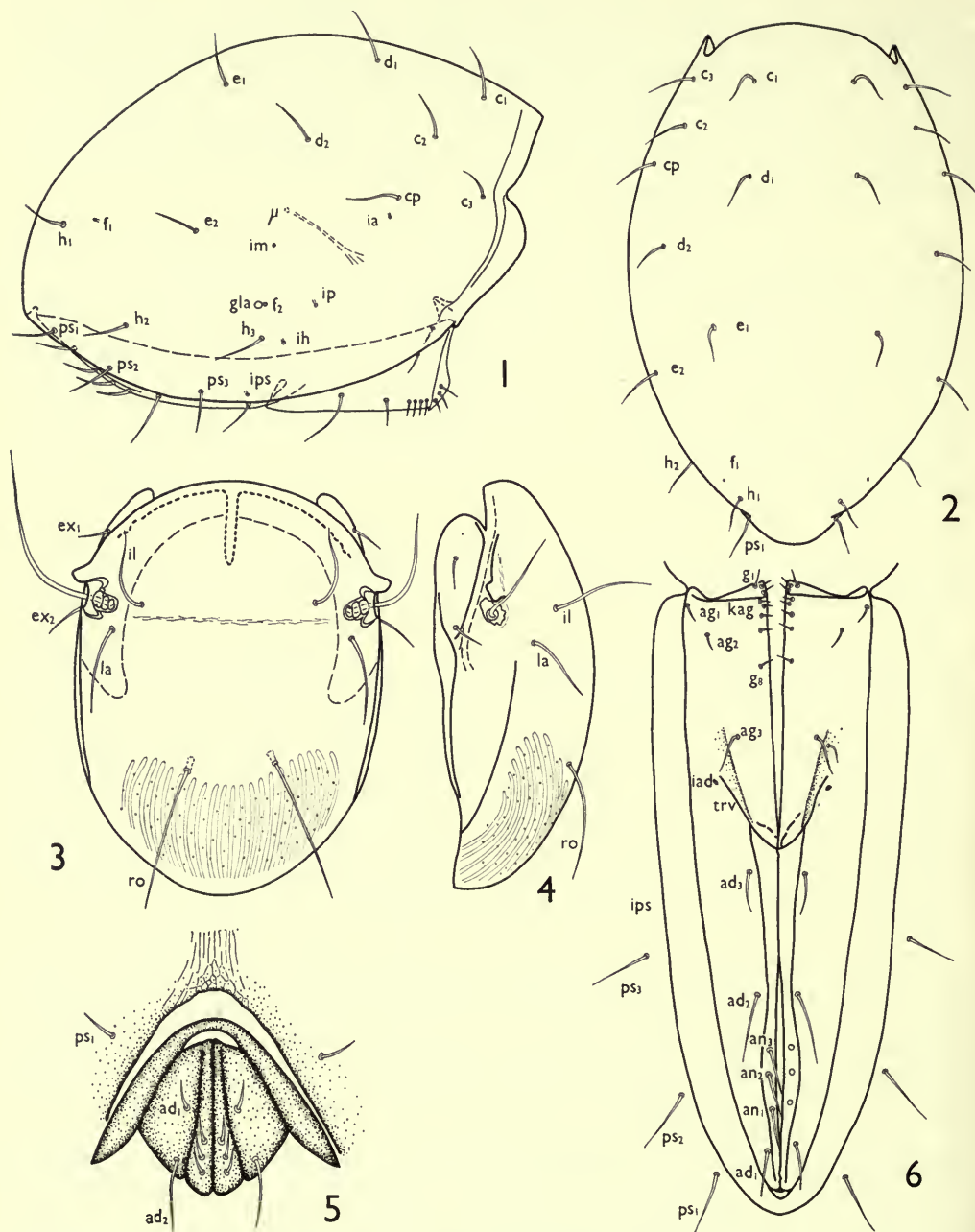
tive spots of variable size. There are 14 pairs of moderately long, fine and smooth notogastral setae. All the setae of the *ps* series are located very low down on the notogaster, near the ventral margin, and the setae of the *h* series and the opening of the lateral abdominal gland *gla* are also relatively low in position. The integumental canals of the vestigial setae *f1* and *f2* are clearly visible but the setae were not observed. There are five pairs of notogastral fissures. Anteriorly there is a very deep sensillar notch. μ is a very distinct refractive pigmented cylinder on the inner surface of the integument.

Ano-genital region (Text-figs. 5 and 6): The anterior carina (*kag* of Grandjean, 1967) is well developed and the articulation with the anteroventral angle of the notogaster is simple. The genital plates are completely fused with the ventral plates, but on each side the latter are incompletely divided by an oblique continuation of the ano-genital cleft (*trv*). On the paraxial side of this there is a slightly oblique (almost longitudinal) ridge which extends from the ano-genital border to approximately the level of the posterior aggenital setae. There are eight pairs of short genital setae arranged in a pattern of $7 + 1$ on the paraxial border, and three pairs of aggenital setae; two anterior and one posterior. In the figured specimen there are two posterior aggenital setae on the left side. There are three pairs of sub-equal genital papillae, and the genital plates fuse to form a narrow bridge posteriorly. An internal thickened curved apodeme ("*verbindungsbrücke*" of Märkel, 1964) is also present.

The anal plates are for the most part discrete although near their posterior extremities they are fused, without a suture line, with the ventral plate. There are three pairs of anal setae, markedly posterior in position, and three pairs of longer adanal setae which are inserted close to the paraxial border of the ventral plate. The adanal fissure (*iad*) lies very far forward near the end of the oblique cleft (*trv*) in the ventral plate. There is a small clear crescent-shaped sinus between the posterior margin of the ventral plate and the plicature plate (Text-fig. 5). A shallow sinus is also located between the posterior border of the plicature plate and the notogaster, and in the region of this sinus the notogastral integument is striated and reticulated.

Infracapitulum (Text-fig. 7): Typically euphthiracaroid in form; stenarthrous and the rutella with atelabasic expansions (Grandjean, 1957). Setae *a*, *m*, and *h* are long and smooth, and the supra-coxal setae (*e*) are short and smooth. There are three pairs of adoral setae. Setae *or*₁ (Text-fig. 10) are forked, the antiaxial branch being curved and serrated, the paraxial straight and barbed. Setae *or*₂ and *or*₃ are weakly serrated, *or*₂ being straight and *or*₃ strongly curved.

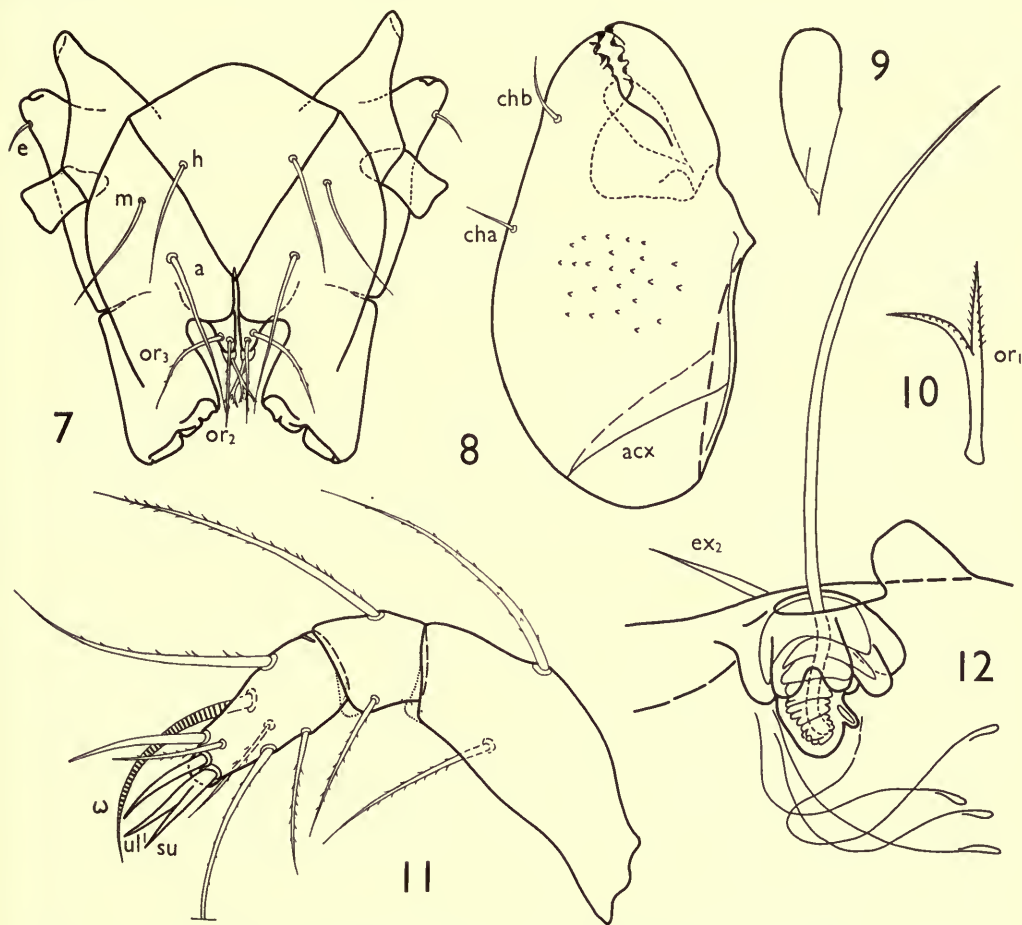
Chelicerae (Text-fig. 8): Approximately 260 μ m in length. The fixed digit has six teeth and the movable five. An obtuse smooth membranous process arises on the paraxial surface from near the base of the movable digit (Text-fig. 9) and this is almost certainly homologous with the structure which van der Hammen (1968) has called the paraxial oncophysis of the principal segment. The membrane attachment line (*acx*) is markedly posterior in position. The cheliceral integument is punctate



FIGS. 1-6. *Terratriitia askewi* gen. et sp. nov. 1, Notogaster, lateral. 2, Notogaster, dorsal. 3, Aspis, dorsal. 4, Aspis, lateral. 5, Notogaster, anal and adanal plates; posterior aspect. 6, Venter.

posteriorly and porose anteriorly and on both the paraxial and antiaxial surfaces it is furnished with a number of small spines, about 30 on the paraxial surface and about 20 on the antiaxial. Setae *cha* and *chb* are smooth, *chb* being slightly longer than *cha*.

Palps (Text-fig. 11): Three-segmented, with the setal formula (2-2-9). Four of the setae on the tarsus are eupathidial and two of these, *ul'* and *su*, are fused basally.



FIGS. 7-12. *Terratritia askewi* gen. et sp. nov. 7, Infracapitulum. 8, Chela. 9, Paraxial oncophysis of the principal cheliceral segment. 10, Seta *or*₁. 11, Palp. 12, Bothridium and sensillus.

Legs (Text-figs. 13-17): All the legs are triheterodactyl and the setal and solenidial formulae are as follows:

- I (1-3-5-5-21) and (2-1-3);
- II (1-4-4-5-13) and (1-1-2);
- III (2-3-3-3-11) and (1-1-0);
- IV (2-3-2-2-9) and (0-1-0).

Leg I is very stout—almost crassate. The lateral claws on all the legs are slender but spatulate and they carry a row of dorsal barbs. On genu I solenidia σ_1 and σ_2 are closely associated with the dorsal and paraxial lateral setae, respectively, and the solenidia on genera II and III and those on all the tibiae are closely associated with the dorsal setae of the respective segments. These “coupling setae”, however, have their own integumental canals. On tarsus I (Text-figs. 13 and 17) solenidion ω_3 lies proximally in relation to the famulus and the latter is closely associated with ω_1 . ω_2 , the largest of the solenidia on tarsus I has a well-developed distal coupling seta.

Egg: One specimen contained seven slender eggs. The chorion is smooth with no sign of sculpturing.

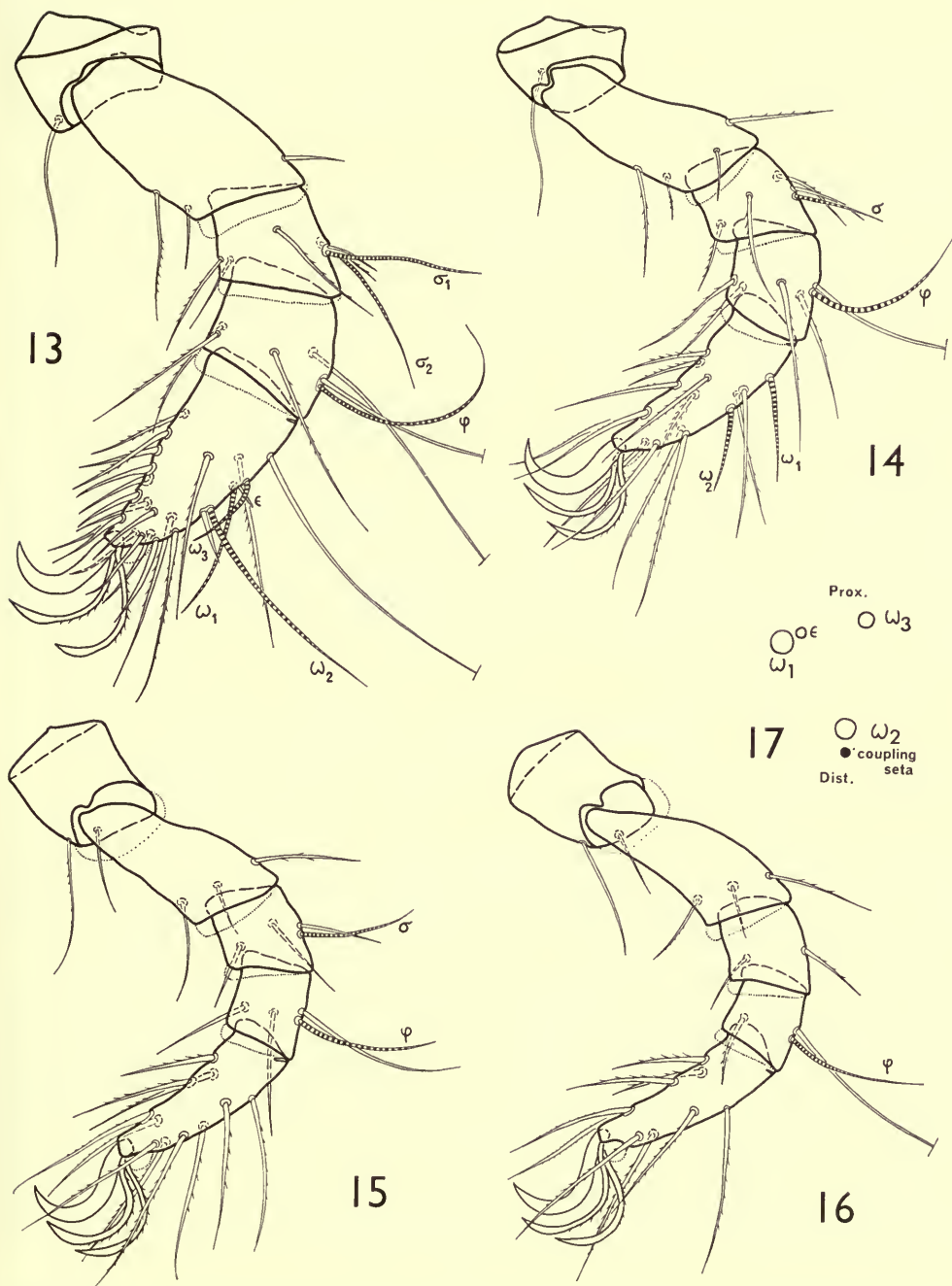
Material: Holotype female, B.M.(N.H.) Reg. No. 1968 : 729, and three paratypes, B.M.(N.H.) Reg. No. 1968 : 730, from sample B161. Paratype, B.M.(N.H.) Reg. No. 1968 : 731, from sample B74.

SYSTEMATIC POSITION

Sellnick (1959) proposed the genus *Austrotritia*, with *Austrotritia quadricarinata* Sellnick as type, and with the following diagnosis: “This genus is a member of the subfamily Euphthiracarinae Jacot. Genital shields and adgenital shields fused without suture. There is a very long deep indentation between the adgenital and adanal shields, directed outward and forward, but not reaching the outer border of these shields”.

Within the terms of Sellnick's concept of the genus, *Terratritia askewi* should clearly be classified in *Austrotritia*, and in the preliminary numerical taxonomic survey (Sheals, *op. cit.*), where it was referred to as “unit 4”, it was initially, although tentatively placed in this genus. However, an analysis of the matrix of similarity coefficients using the single-linkage cluster method (Sneath, 1957) showed *Terratritia askewi* to be the most isolated euphthiracaroid unit in the study, and its affinities, such as they were, lay mostly with the *Mesotritia*/*Perutritia* group which it joined at the 76% similarity level. For comparison, it can be noted that all the Euphthiracaroida examined came together at the 74% phenon line, *Austrotritia lebronneci* (Jacot) and *Indotritia acanthophora* Märkel joined at the 88% level, and three species of *Oribotritia*, including *O. berlesei* (Michael), the type species, joined the *A. lebronneci*/*I. acanthophora* group at the 84% level. As will be noted below, even on the basis of overall similarity, there is good reason to regard *A. lebronneci* as being congeneric with *A. quadricarinata* and the detailed descriptions of *Indotritia* species given by Märkel (1964) provide a sound basis for considering *I. acanthophora* to be congeneric with *Tritia krakatauensis* Sellnick, the type species of *Indotritia* Jacot.¹ Thus, the dissimilarity between *Terratritia* and *Austrotritia* is much greater than the dissimilarity between *Austrotritia* and *Indotritia* and much greater also than the

¹We are informed by Dr. M. Sellnick that the type material of *Tritia krakatauensis* has been destroyed. A subspecies, *Indotritia krakatauensis consimilis*, from Yugoslavia is described by Märkel (*op. cit.*).



FIGS. 13-17. *Terratritia askewi* gen. et sp. nov. Legs. 13, Leg I. 14, Leg II. 15, Leg III. 16, Leg IV. 17, Tarsus I, dorsal aspect of proximal region.

dissimilarity between either of these genera and *Oribotritia*. If *Terratritia askewi* were to be accommodated in an existing oribotritiid genus it would have to be referred to *Mesotritia* Forsslund but obviously the gap is too well marked to justify this classification.

Terratritia can be defined as an oribotritiid with the following combination of characters:

1. Genital and ventral plates completely fused.
2. Ventral shield on each side incompletely divided by an oblique cleft which is a continuation of the cleft separating the anal and genital plates.
3. Setae ps_1 very low in position, inserted close to the posterior ventral angle of the notogaster.
4. Solenidion ω_2 on tarsus I inserted distally in relation to solenidion ω_1 , famulus closely associated with ω_1 .
5. Solenidia of tarsus II uncoupled. Solenidion ω_1 of tarsus II inserted proximally in relation to setae *ft*.

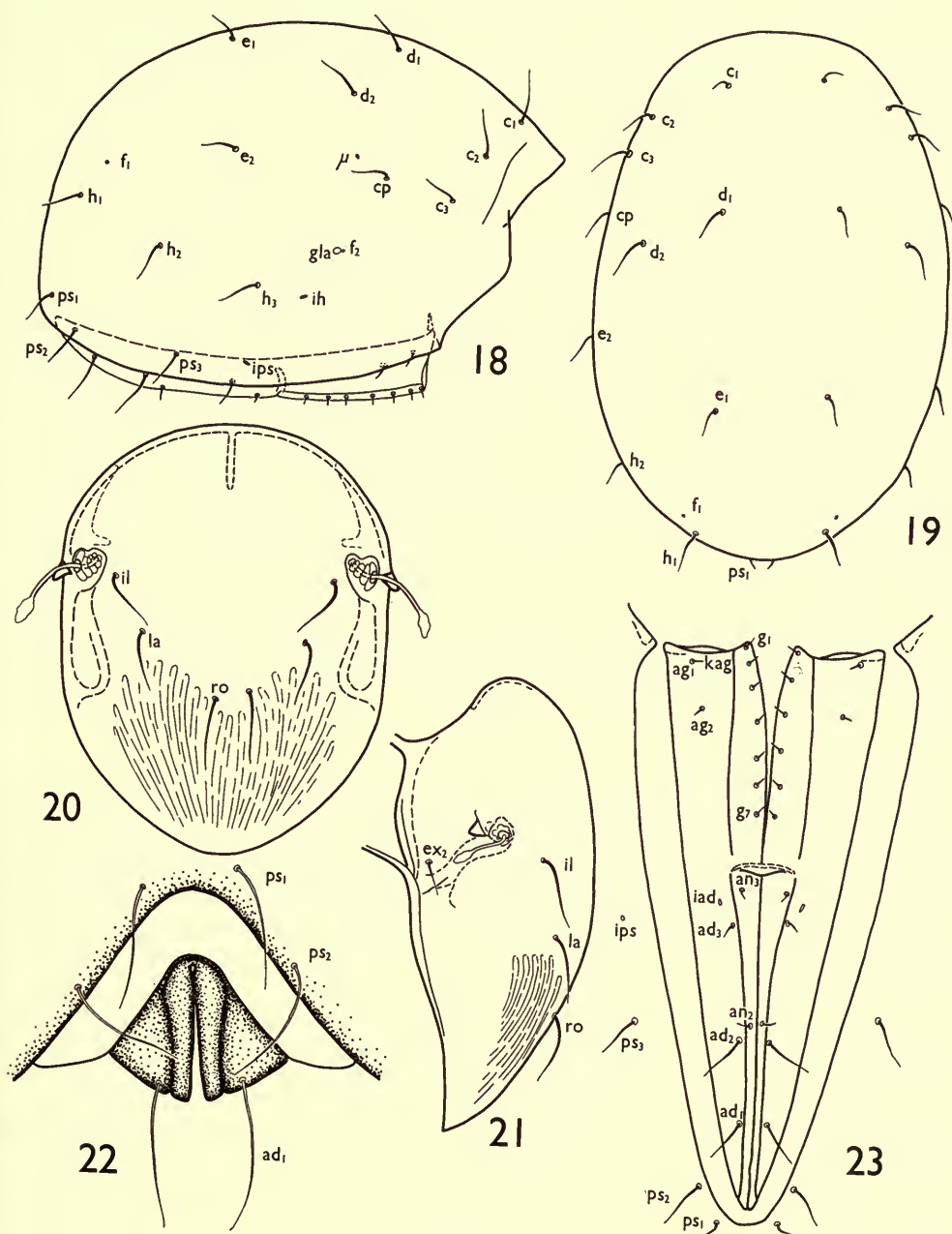
In relation to attributes 1 and 2, it is interesting to find that despite their prominence these "genital aggenital" features (hitherto regarded as being diagnostic for *Austrotritia*) are not sufficiently good "marker" characters to be used without reference to other attributes. In other words these features are not highly correlated with many other characters, and hence they are not, in the words of Huxley (1877) "a mark of many likenesses or unlikenesses".

Sabacarus corneri gen. et sp. nov.

The two specimens available for study were pale and almost colourless.

Aspis (Text-figs. 20 and 21): 200 μm long, 160 μm wide and with a greatest depth of 80 μm . The integument is generally finely porose smooth and the rostral area carries a pattern of longitudinal striations. There are no lateral carinae although the *aspis* rim is thickened laterally. A posterior median apodeme ("scheitelbalken") is present and a small sub-triangular scale lies behind and below the bothridium. All the dorsal setae are fine, short and procumbent. The rostral setae (*ro*) are inserted relatively far back and the lamellars (*la*) are widely removed from the lateral margin. The interlamellar setae (*il*) are paraxial in relation to the bothridia. The bothridium (Text-fig. 29) is curved, and in lateral view is seen to lie in a transverse thickening of the *aspis*. It has a small number of relatively large chambers. The outer chamber is the largest, and the inner chambers are porose. No tracheoles could be discerned. The sensillus is relatively short, membranous and dilated distally. In the material examined only the anterior exobothridial setae (*ex*₂) were present although the alveoli of the posterior pair could be seen.

Notogaster (Text-figs. 18 and 19): Diagonal length 350 μm , with a greatest depth of 250 μm and a greatest width of 240 μm . Rounded posteriorly. Excluding



FIGS. 18-23. *Sabacarus corneri* gen. et sp. nov. 18, Notogaster, lateral. 19, Notogaster, dorsal. 20, Aspis, dorsal. 21, Aspis, lateral. 22, Notogaster, anal and adanal plates; posterior aspect. 23, Venter.

vestiges there are 14 pairs of fine relatively short notogastral setae. Fissure *ih* and the opening of the lateral abdominal gland (*gla*) are markedly anterior in position. Setae *ps*₁ are inserted very low down near the postero-ventral angle. Fissures *ia*, *im* and *ip* are absent and the vestigial *f*₂ lies immediately in front of, and contiguous with *gla*. μ is a pigmented spot on the inner surface of the integument.

Ano-genital region (Text-figs. 22 and 23). The anterior carina (*kag*) is weak and the articulation of the ventral shield with the antero-lateral angle of the notogaster is simple, with no hook-like process. The genital plates are discrete and completely delimited antiaxially by a distinct suture. There are six to seven pairs of small more or less evenly-spaced submarginal genital setae and two pairs of small aggenital setae. The genital plates are fused posteriorly to form a narrow bridge and an internal curved apodeme (" *verbindungsbrücke* ") is present. The anal plates are for the most part discrete, and completely delimited antiaxially. They are slender but widen anteriorly. They also widen slightly posteriorly and fuse with each other terminally (Text-fig. 22). The ventral plates on either side are reduced posteriorly and are barely contiguous with each other at the plicature. There are two pairs of small anal setae presumably *an*₂ and *an*₃ and three pairs of adanal setae. Setae *ad*₁ and *ad*₂ relatively long while *ad*₃ are short. The adanal fissure (*iad*) is conspicuous and situated in front of seta *ad*₃. The ventral plicature terminates in a shallow sinus.

Infracapitulum (Text-fig. 24): Typically euphthiracaroid in general form although the antiaxial shoulders of the genae at the palp acetabulum are much broader than usual. There are only two pairs of adoral setae. *or*₁ are brush like distally, while *or*₂ are smooth and slender.

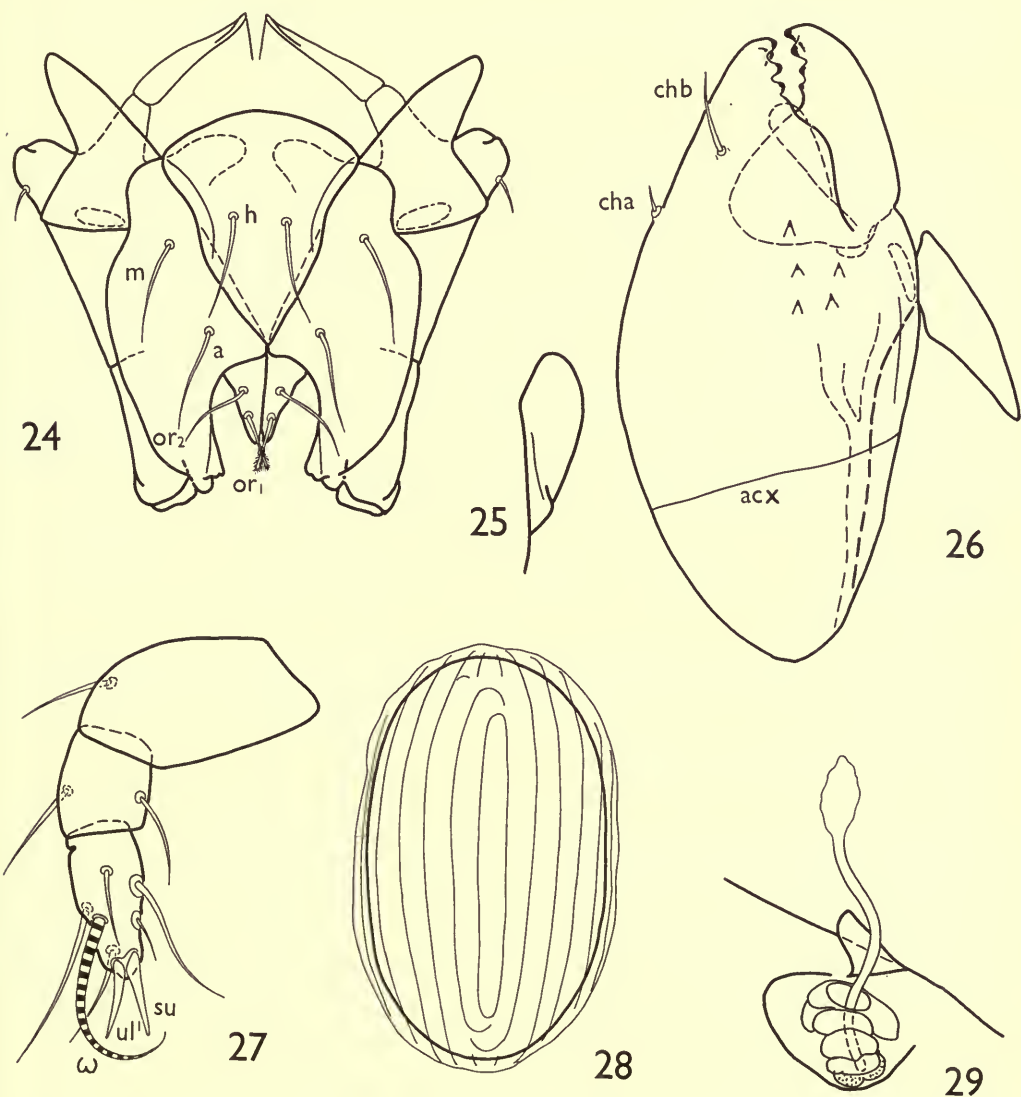
Chelicerae (Text-fig. 26): 125 μ m in length. Both the fixed and the movable digits have four teeth and the paraxial oncofysis of the principal segment (Text-fig. 25) is smooth. The membrane attachment line (*acx*) is faint. The cheliceral integument is porose and the principal segment carries a few relatively large spines on both the paraxial and antiaxial surfaces. Setae *cha* are very short and arise from a membranous tubercle. Setae *chb* which are very much longer are inserted well down on the antiaxial face.

Palps (Text-fig. 27): Three-segmented with the setal formula (1-2-7). On the tarsus the anterior ventral seta is very short and there are only two eupathidia.

Legs (Text-figs. 30-34): All the legs are monodactyl and the setal and solenidial formulae are as follows:

- I (1-2-3-5-15) and (2-1-3);
- II (1-2-3-3-11) and (1-1-2);
- III (2-2-2-2-10) and (1-1-0);
- IV (2-2-2-2- 9) and (0-1-0).

The legs are relatively short and thick but legs I and II are considerably more robust than III and IV. On genu I solenidia σ_1 and σ_2 are associated with the dorsal setae and paraxial lateral setae respectively and on genu II and genu III the solenidia are associated with dorsal setae. However, all these companion setae have their own integumental canals. The solenidia on the tibiae are associated with the dorsal setae but again the companion setae are appreciably removed from the solenidia and have their own integumental canals. On all the tibiae the dorsal setae are



FIGS. 24-29. *Sabacarus corneri* gen. et sp. nov. 24, Infracapitulum. 25, Paraxial oncophysis of the principal cheliceral segment. 26, Chela. 27, Palp. 28, Egg. 29, Bothridium and sensillus.

very much longer than the solenidia. On tarsus I solenidion ω_1 lies distally in relation to ω_2 and ω_3 is proximal to ω_2 (Text-fig. 33). The famulus is relatively large, verrucose, tapered and hooked distally. It is relatively closely associated with ω_2 . None of the tarsal solenidia has a coupling seta.

Egg (Text-fig. 28): A single, relatively large egg ($190 \times 120 \mu\text{m}$) was present in one specimen. The chorion is patterned with a series of deep longitudinal grooves.

Material: Holotype female, B.M.(N.H.) Reg. No. 1968 : 736 and one paratype female, B.M.(N.H.) Reg. No. 1968 : 737 from sample B124.

SYSTEMATIC POSITION

After using the results of a fairly elaborate numerical analysis to justify the proposal of *Terratritia* it is with some hesitation that a new genus is proposed for this species without evidence from a similar study. *S. corneri* has obvious affinities with *Protoribotritia*, particularly in relation to the form of the venter, the general shape of the aspis and in relation to certain leg features, but its accommodation in this genus would necessitate modifying the concept of what is already a very heterogeneous assemblage. Moreover, many of the differences observed in *S. corneri* relate to attributes which in other oribotritiids appear to be good marker characters, notably the solenidiotaxy of leg IV and the position of seta ps_1 . *S. corneri* also has affinities with *Mesotritia* but a widening of the concept of this genus would necessitate a re-evaluation of the related genera *Perutritia* and *Maerkelotritia*.

Sabacarus can be defined as an oribotritiid with the following combination of characters:

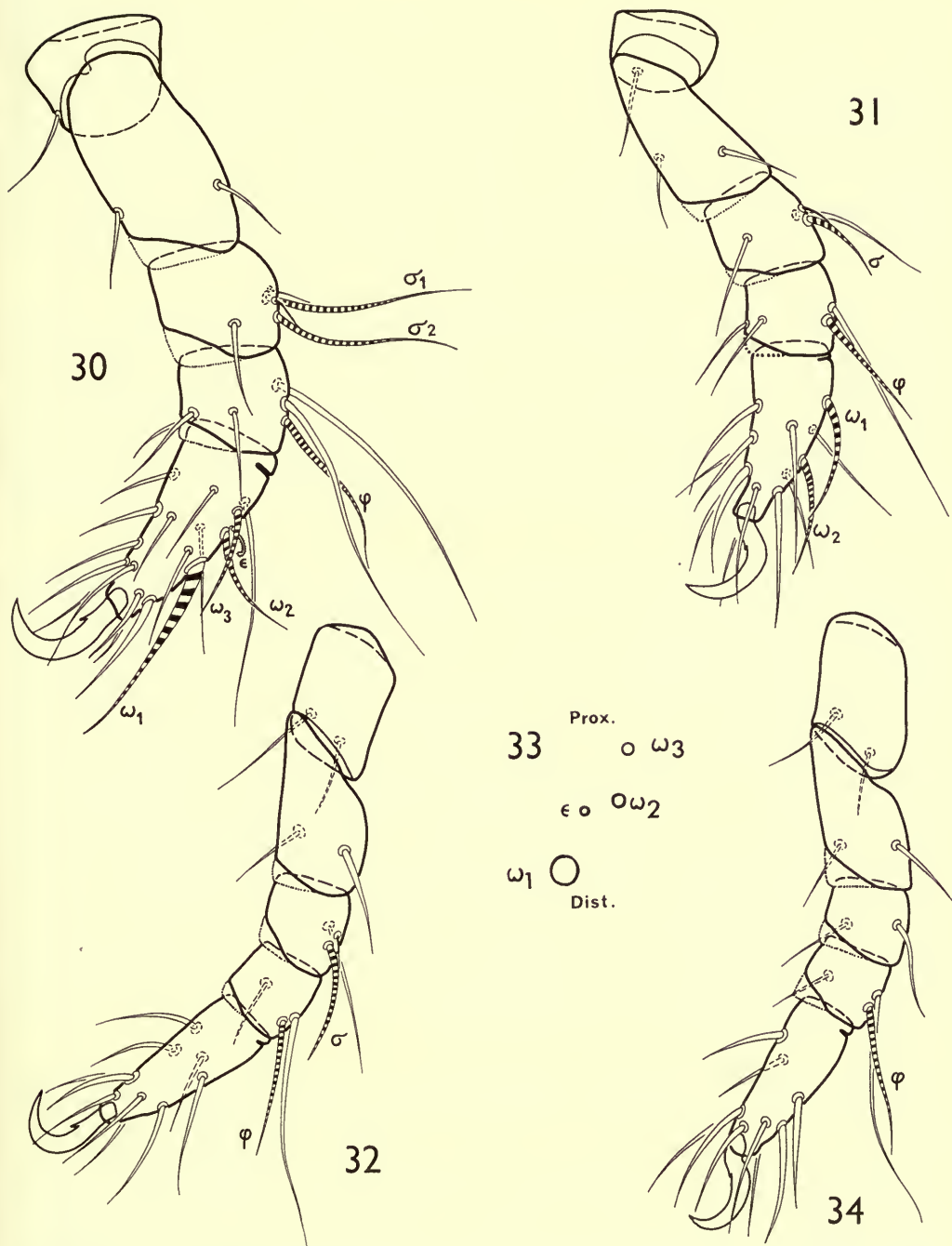
1. Legs monodactyl.
2. Genital plates discrete, completely delimited antiaxially by a distinct fissure.
3. Setae ps_1 very low in position, inserted close to the posterior ventral angle of the notogaster.
4. Genu IV without a solenidion.

Whilst the presence of this combination of characters is sufficient to distinguish *Sabacarus* from other oribotritiid genera, it can also be noted that setae d on all the tibiae are very long and exceed the length of the tibial solenidia. This is unusual in the Oribotritiidae, for on tibiae II–IV very long dorsal setae have been observed only in *Mesotritia*. The presence of a very long paraxial lateral seta on tibia I is also interesting, although this seta is also long in *Oribotritia*, *Mesotritia* and *Perutritia*.

Austrotritia kinabaluensis sp. nov.

The two specimens available for study were pale brown in colour.

Aspis (Text-figs. 37 and 38): $350\text{--}475 \mu\text{m}$ long, $260\text{--}340 \mu\text{m}$ wide and $140\text{--}150 \mu\text{m}$ deep. Straight sided and pointed anteriorly. The integument is finely porose and



FIGS. 30-34. *Sabacarus corneri* gen. et sp. nov. Legs. 30, Leg. I. 31, Leg. II. 32, Leg. III. 33, Tarsus I, dorsal aspect of proximal region. 34, Leg. IV.

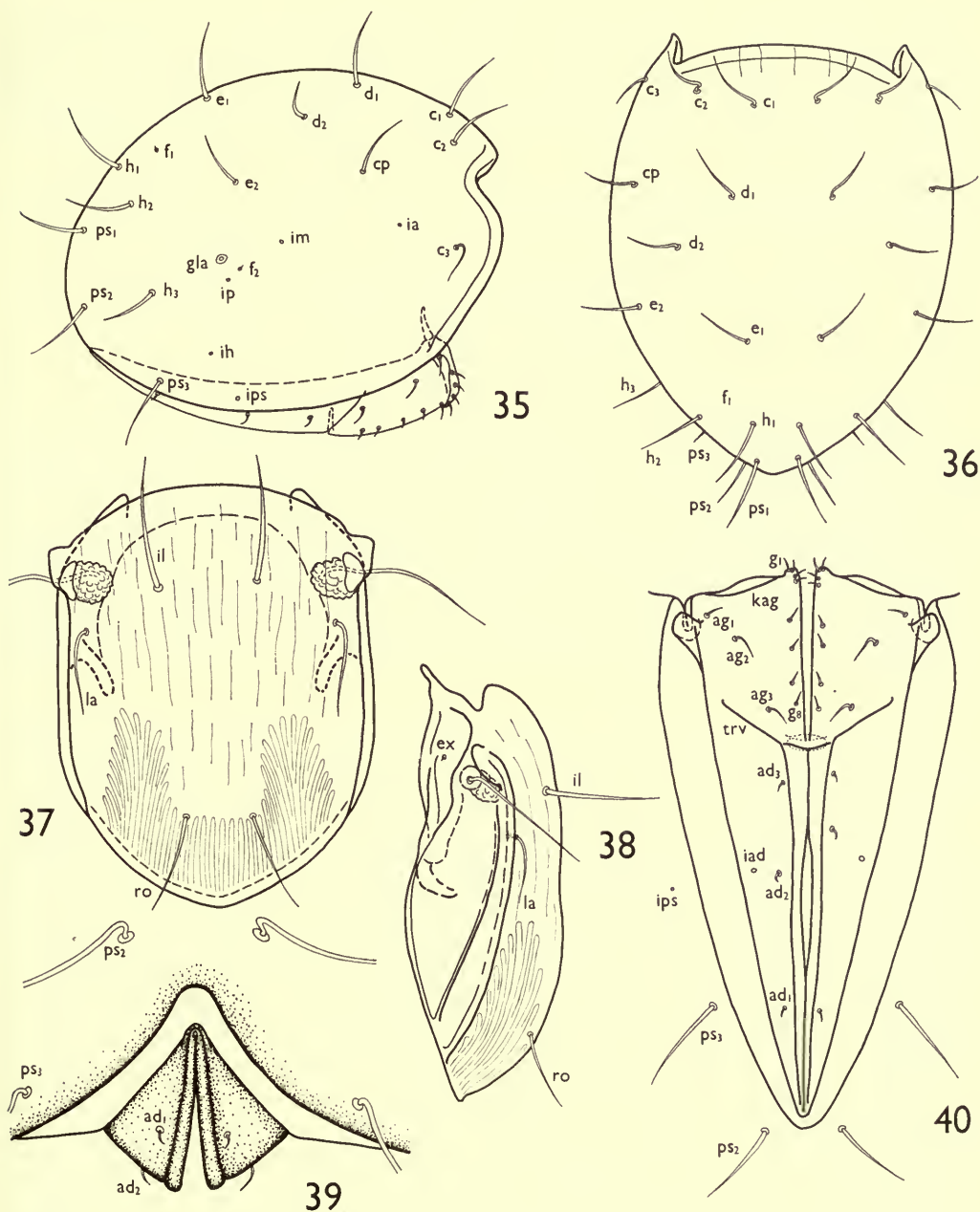
there are longitudinal striations over the whole surface. Additionally, the rostral area is patterned internally with granular striations. There are two lateral carinae but the posterior median apodeme (" *scheitelbalken* ") is absent. A large bothridial scale lies above and slightly behind the sensillus. The rostral setae (*ro*) are semi-erect and extend beyond the margin of the rostrum. The lamellar setae (*la*) are procumbent and inserted close to the lateral margin while the interlamellar setae (*il*) are strongly erect and fairly widely removed from the bothridium. The bothridium (Text-fig. 46) has a large outer chamber and an inner chamber with numerous alveoli. No tracheoles could be discerned. The sensillus is long, smooth and flagelliform and there is a single, almost vestigial, exobothridial seta.

Notogaster (Text-figs. 35 and 36): Diagonal length 580–1,000 μm with a greatest depth of 440–750 μm and a greatest width of 440–725 μm ; relatively wide and pointed posteriorly. The integument is porose and smooth with longitudinal striations over most of the surface. Excluding *f*₁ and *f*₂, which contain distinct but vestigial setae, there are 14 pairs of relatively long curved notogastral setae. Setae *ps*₁ are fairly high in position. The sensillar notch is well marked and high in position and there are five pairs of notogastral fissures. *f*₂ is well separated from *gla*. The notogastral mark μ could not be discerned.

Ano-genital region (Text-figs. 39 and 40): The anterior carina (*kag*) is well developed and the ventral plate articulates with the antero-ventral angle of the notogaster by means of a prominent process with a thickened internal hood-like structure. The genital plates are completely fused with the ventral plates, but on each side the latter are incompletely divided by an oblique continuation of the ano-genital cleft. (*tru*). There are eight pairs of small sub-marginal genital setae arranged in two groups; a cluster of four near the anterior border and a posterior series of four; more or less evenly spaced. There are three pairs of aggenital setae, *ag*₁ being smaller than either of the other two. The posterior margin of the genital opening is bridged by an internal apodeme (" *verbindungsbrücke* "). The genital plates are fused posteriorly to form a narrow bridge. The anal plates are discrete, and the ventral plates, on each side, are joined behind them. There are no anal setae and the three pairs of sub-marginal adanal setae are minute. The adanal fissure *iad* near the antiaxial margin at about the level of notogastral fissure *ips*. Posteriorly the cleft between the anal plates terminates in a pore and there is a shallow sinus at the posterior termination of the ventral plicature.

Infracapitulum (Text-fig. 41): Typically euphthiracaroid. There are three pairs of adoral setae, *or*₁ being brush-like distally and *or*₂ and *or*₃ smooth and slender.

Chelicerae (Text-fig. 43): About 200 μm in length. Both the fixed and movable digits of the chelicerae have four teeth and the paraxial oncofysis of the principal segment (Text-fig. 44) has a row of about 14 conical spines. This oncofysis is elongated and at its base the outline of another membranous structure, possibly the ventral oncofysis, could be discerned. Setae *cha* and *chb* are both smooth, *cha*



FIGS. 35-40. *Austrotrititia kinabaluensis* sp. nov. 35, Notogaster, lateral. 36, Notogaster, dorsal. 37, Aspis, dorsal. 38, Aspis, lateral. 39, Notogaster, anal and adanal plates; posterior aspect. 40, Venter.

being longer than *chb*. The integument on both the paraxial and antiaxial surfaces of the principal segment carries a number of small spines.

Palps (Text-fig. 45): Essentially three-segmented although the femur has two circumsegmental lines separating proximal trochanteral and distal genual regions. Muscle from the tibia inserts in the two distal regions i.e. in the "femur" and "genu". The setal formula is (2-2-9) and four of the setae on the tarsus are eupathidial.

Legs (Text-figs. 50-54): All the legs are triheterodactyl and the setal and solenidial formulae for the holotype are as follows:

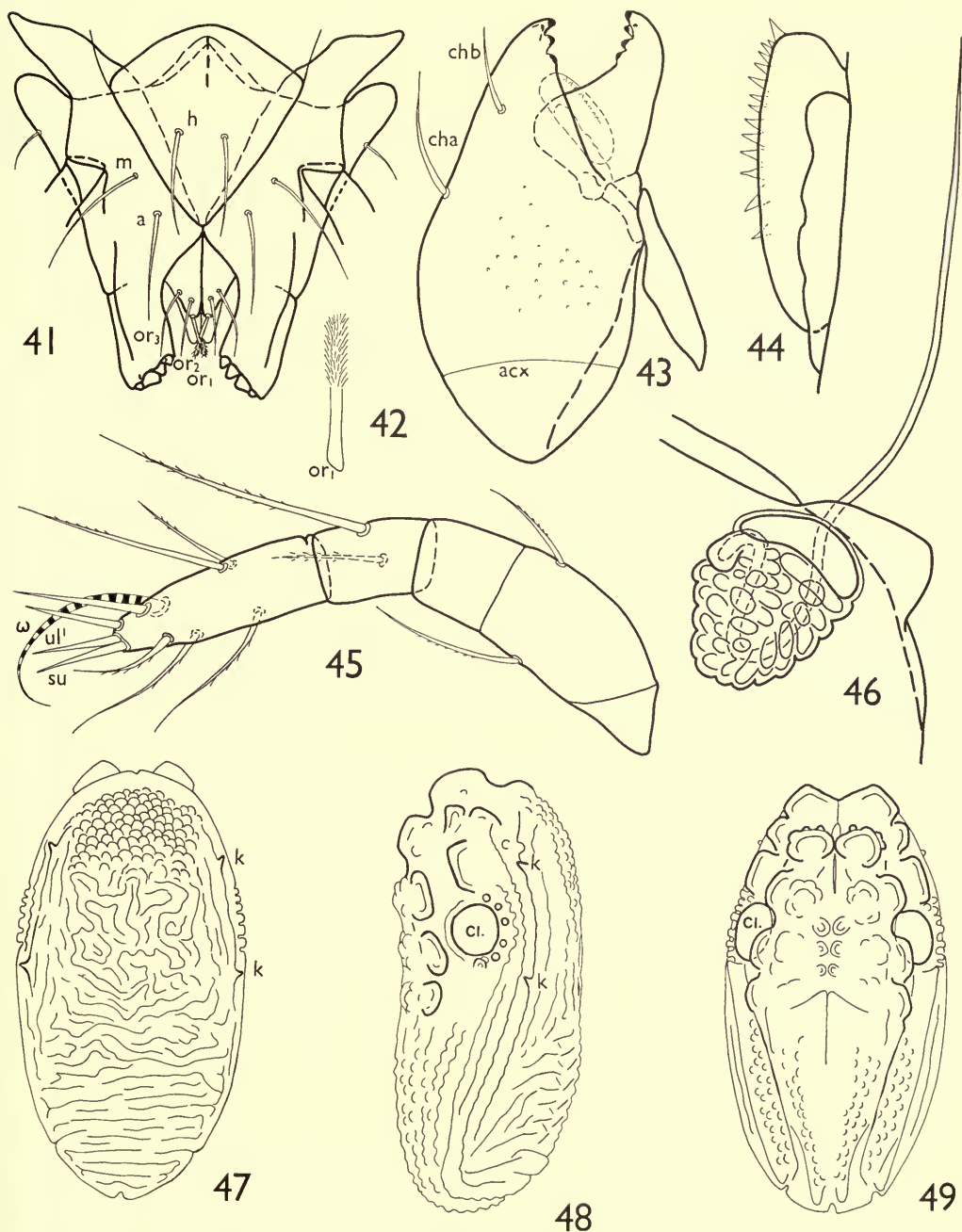
- I (1-4-5-5-21) and (2-1-3);
- II (1-4-4-3-17) and (1-1-2);
- III (3-2-3-3-14) and (1-1-0);
- IV (3-2-2-3-11) and (1-1-0).

On one side genu III had four setae and tarsus III, 13.

On genu I σ_1 and σ_2 are coupled with the dorsal and paraxial lateral setae, respectively, and the solenidia on genua II-IV and those on all the tibiae are coupled with dorsal setae. All the coupling setae are short and do not have separate integumental canals. On tarsus I solenidion ω_3 lies proximally in relation to ω_1 and ω_2 (Text-fig. 53). The distal solenidion ω_2 has a distal coupling seta. The famulus is very closely associated with ω_2 , lying in the same integumental base. Dorsally, femur I has a distal sub-apical cusp and on tarsus II both the solenidia are coupled with setae *ft*. On tarsus IV the paraxial unguinal seta is swollen and almost claw-like.

Egg: The single female contained 23 cylindrical eggs in various stages of development. The eggs were 250-300 μm long and 125-160 μm wide. The chorion, which was smooth, appeared to be shed before the development of the prelarva.

Prelarva (Text-figs. 47-49): The prelarva in many respects is similar to the prelarva of *Oribotritia berlesei* (Michael) (see Grandjean, 1962) nevertheless a number of rather striking differences have been noted and these may be important at generic level. The deep longitudinal folds and grooves which completely cover the dorsum and sides of the prelarva of *O. berlesei* only occur on the sides on *A. kinabaluensis*. Here the dorsum is tuberculate anteriorly, wrinkled in the middle and transversely grooved or wrinkled posteriorly. In the *A. kinabaluensis* prelarva there is more tuberculation ventrally and the organ of Claparède (*Cl*) is much more prominent and has a conspicuous arc of tubercles dorsally. The rostrum is rounded and swollen (not a sharp projection as in *O. berlesei*), and the form of the appendages, especially the rounded cheliceral rudiment (angular in *O. berlesei*), is also rather different. On each side, two teeth (*k*) are present on one of the longitudinal folds above the organ of Claparède. One of the teeth lies in front of this organ and the other behind. Teeth are not present in this position in *O. berlesei* although in the latter an anterior ventral carina with a single tooth on each side is located between the rostrum and the cheliceral rudiments.



FIGS. 41-49. *Austrotrititia kinabaluensis* sp. nov. 41, Infracapitulum. 42, Seta *or*₁. 43, Chela. 44, Paraxial oncophysis of the principal cheliceral segment. 45, Palp. 46, Bothridium and sensillus. 47, Prelarva, dorsal. 48, Prelarva, lateral. 49, Prelarva, ventral.

MATERIAL: Holotype male, B.M.(N.H.) Reg. No. 1968 : 734 from sample B124 and one paratype female, B.M. (N.H.) Reg. No. 1968 : 735 from sample B74.

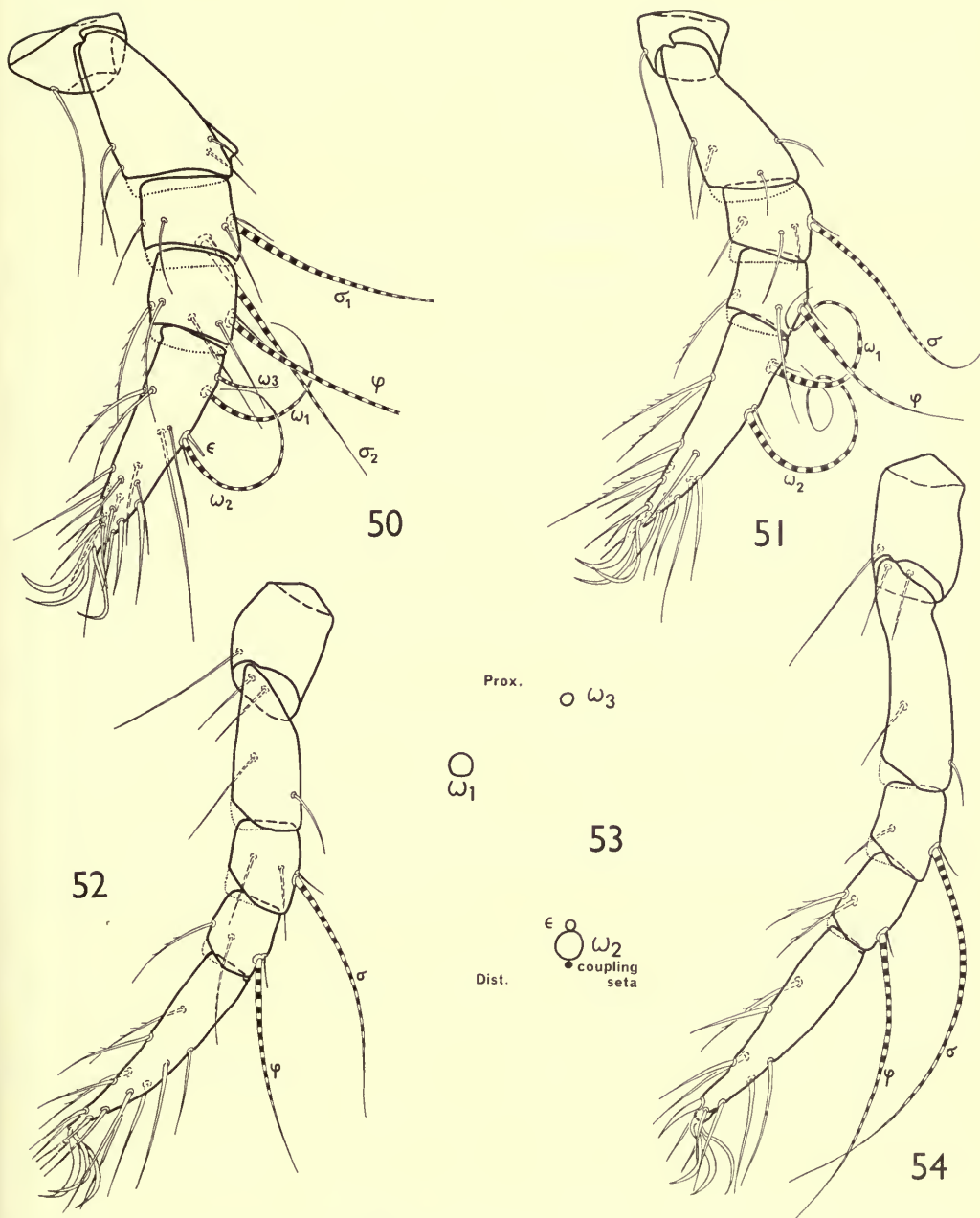
SYSTEMATIC POSITION

It has been noted above that the features of the genital and ventral plates (genital plates completely fused with the ventral plates and the latter partially divided by an oblique cleft) are, when considered alone, insufficient to characterize *Austrotritia*. Through the courtesy of Dr. Nixon A. Wilson of the Bernice P. Bishop Museum, Honolulu, we have been able to examine the holotype of *Austrotritia quadricarinata* Sellnick, the type species of the genus. The specimen is dissected and the parts are mounted in gum chloral on five slides. After soaking off the notogaster (which is badly torn) and examining it in a lactic acid preparation we have found that the distribution of the notogastral setae in the holotype is very similar to that figured for *A. kinabaluensis*. In particular setae ps_1 are inserted high on the notogaster and ps_2 (which are on a fragment of the notogaster attached to the separately mounted venter) lie close to, but above the postero-ventral angle. On the left palp, the femur has two circumsegmental lines separating trochantal and genual regions, but on the right palp femur, while the trochantal region is clearly separated, the distal circumsegmental line is indistinct. The chaetotaxy of the palp in the holotype is similar to that of *A. kinabaluensis*. Legs IV of the *A. quadricarinata* holotype are unfortunately missing, but while several setae are missing on the remaining six legs it is clear that the basic chaetotactic pattern is similar to that noted for *A. kinabaluensis*. It is interesting to note that femur I of *A. quadricarinata* has a distal sub-apical cusp dorsally, moreover, the solenidia on tarsus II are coupled with setae *ft*, the latter being much reduced in length.

We have also been able to examine material of an *Austrotritia* species from Guadalcanal in the Solomon Islands, which after comparison with the syntype series (six badly damaged specimens mounted in Canada Balsam) we consider to be very close to, if not conspecific with, *Austrotritia lebronneci* (Jacot). In this species also the distribution of notogastral setae is very similar to that shown for *A. kinabaluensis*. Seta ps_1 is inserted fairly high, higher in fact than shown in Jacot's figure (Jacot, 1935). Moreover, femur I has a dorsal sub-apical cusp, the solenidia on tarsus II are coupled with setae *ft* and on tarsus IV the paraxial unguinal seta is swollen and almost claw-like.

It seems therefore that *Austrotritia* can be defined as an oribotritiid genus with the following combination of characters:

1. Genital and ventral plates completely fused.
2. Ventral plate on each side incompletely divided by an oblique cleft which is a continuation of the cleft separating the anal and genital plates.
3. Setae ps_1 inserted fairly high on the notogaster, well removed from the posterior-ventral angle.
4. On tarsus I solenidion ω_2 inserted distally in relation to ω_1 . Famulus associated with ω_2 .
5. On tarsus II solenidia are coupled with setae *ft*.



FIGS. 50-54. *Austrotritia kinabaluensis* sp. nov. Legs. 50, Leg. I. 51, Leg. II. 52, Leg. III. 53, Tarsus I, dorsal aspect of proximal region. 54, Leg. IV.

Additionally, in the type species, and in the two other species examined, femur I has a dorsal sub-apical cusp, and in two species the paraxial unguinal seta on tarsus IV is swollen. The form of the setae on tarsus IV of the type species is not known. These additional features may well be constant within the genus but they are known to occur also in at least one species of *Indotritia*, *I. acanthophora* Märkel. (The swollen unguinal seta on tarsus IV is not noted by Märkel, evidently because legs IV in his specimen were damaged, but we have seen this feature in material of *I. acanthophora* collected in Jamaica).

Oribotritiidae: Key to Genera

The family Oribotritiidae is now made up of ten genera which can be separated as follows:

- 1 Ventral plate on each side incompletely divided by an oblique cleft (*trv*) which runs from the junction of the anal and genital plates 2
- Ventral plate without an oblique cleft. 5
- 2 Genital plates completely fused with ventral plates 3
- Genital plates delimited antiaxially by a complete or incomplete suture 4
- 3 On tarsus II setae *ft* short and coupled with the solenidia (Text-fig. 51). Setae *ps*₁ inserted relatively high on the notogaster remote from the postero-ventral angle. Femur I usually with a dorsal sub-apical cusp (Text-fig. 50)

AUSTROTRITIA Sellnick, 1959
(Type: *Austrotritia quadricarinata* Sellnick, 1959)

On tarsus II setae *ft* long and not coupled with the solenidia (Text-fig. 14). Setae *ps*₁ inserted low down on the notogaster near the posterior ventral angle. Femur I without a dorsal subapical cusp

TERRATRITIA gen. nov.
(Type: *Terratritia askewi* sp. nov.)
- 4 Genital plates completely delimited antiaxially by a suture which reaches the anterior margin of the plates. Setae *ft* on tarsus II long and not coupled with the solenidia 1

ORIBOTRITIA Jacot, 1924
(Type: *Phthiracarus berleseii* Michael, 1898)

– Suture between genital and ventral plates incomplete, not reaching the anterior margin of the plates. On tarsus II setae *ft* usually (probably invariably) short and coupled with the solenidia

INDOTRITIA Jacot, 1929
(Type: *Tritia krakatauensis* Sellnick, 1923)
- 5 Legs monodactyl 6
- Legs triheterodactyl 8
- 6 Genu IV with a solenidion **PROTORIBOTRITIA** Jacot, 1938
(Type: *Protoribotritia canadaris* Jacot, 1938)
- Genu IV without a solenidion 7
- 7 With four pairs of setae in the *ps* series. Genital plates completely fused with ventral plates **PARATRITIA** Moritz, 1966
(Type: *Paratritia baloghi* Moritz, 1966)
- With three pairs of setae in the *ps* series. Genital plates discrete

SABACARUS gen. nov.
(Type: *Sabacarus corneri* sp. nov.)
- 8 Genu IV with a solenidion. Aspis without lateral keels

MAERKELOTTRITIA Hammer, 1967
(Type: *Maerkelotritia alaskensis* Hammer, 1967)

– Genu IV without a solenidion. Aspis with one or two lateral keels 9

- 9 Aspis with two lateral keels. Ventral plicature with a terminal sinus.

PERUTRITIA Märkel, 1964

(Type: *Perutritia amazonensis* Märkel, 1964)

- Aspis with one lateral keel. Ventral plicature with a terminal fissure

MESOTRITIA Forsslund, 1963 s. lat.

a. Notogaster rounded. Terminal fissure short. Median pore present near dorsal margin of fissure. subgen. **MESOTRITIA** Forsslund, 1963

(Type: *Mesotritia testacea* Forsslund, 1963)

b. Notogaster elongate. Terminal fissure long. Median pore absent
subgen. **ENTOMOTRITIA** Märkel, 1964

(Type: *Mesotritia (Entomotritia) piffli* Märkel, 1964)

EUPHTHRACARIDAE Jacot

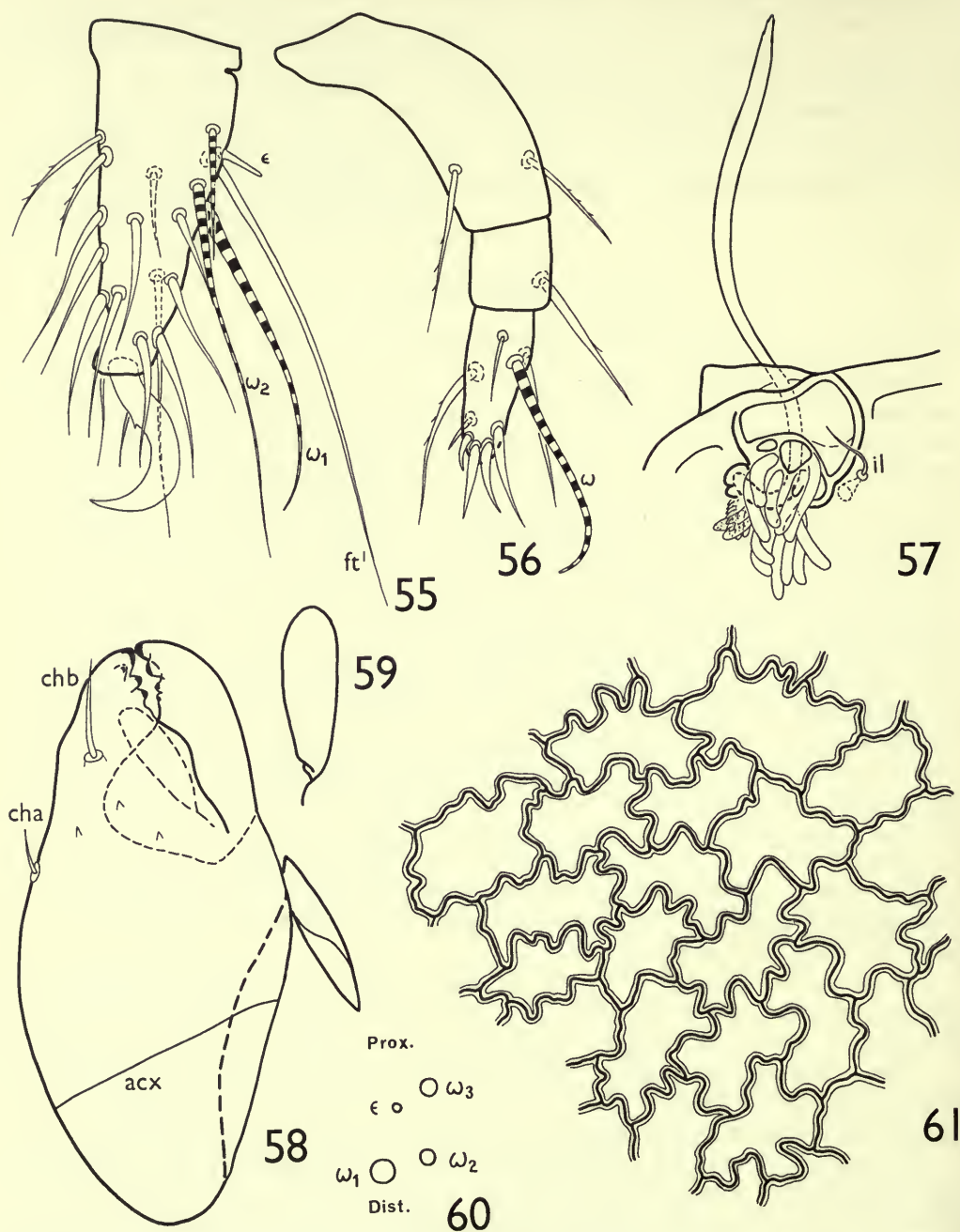
Microtritia tropica dusan subsp. nov.

Microtritia tropica Märkel was collected from soil and litter in a number of localities in Peru (Märkel, 1964). The three specimens (all females) from Borneo fall within the size range given for the Peruvian material and the arrangement of the notogastral setae and fissures appears to be identical in both populations. The pronotal tectum ("tectum pronotique, TPN" of Grandjean, 1967) is not pitted as in some species of *Microtritia*, e.g. *M. incisa* Märkel, and again the general form of the aspis and its setae is very similar in both populations. In the Borneo material, however, the distance between the bases of the rostral setae is almost twice as great as the distance between the bases of the lamellar setae. The rostral basal distance is considerably less in the Peruvian material. Moreover, in the Borneo specimens the interlamellar setae (*il*), which are almost as long as the other setae of the aspis, lie slightly in front of the bothridia (Text-fig. 57), while in the Peruvian material the interlamellar setae are shorter than the other setae of the aspis and are inserted above the bothridia. The bothridium (Text-fig. 57) appears to be similar in both populations. It consists of a large outer chamber and a number of small inner chambers from which alveoli extend as a number of long finger-like extensions reminiscent of a bunch of bananas. No tracheoles could be discerned. The sensillus differs slightly from that of the Peruvian material. It is long, smooth and very slightly clavate and with very slight serrations terminally, and hardly needle-like as in the Peruvian specimens.

The notogaster is smooth with numerous small refractive spots. The notogastral fissures are relatively large and thickwalled as in other members of the genus *Microtritia* and are actually larger than the opening of the lateral abdominal gland. The faint integumental canal of vestigial seta *fi* is near *h*₁ and the canal of *f*₂, also faint, is slightly in front of, but not contiguous with *gla*. μ is a relatively large dense refractive pigmented cylinder on the inner surface of the integument.

The general arrangement of the plates on the venter is characteristic of the genus. As in the typical subspecies there are five pairs of genital setae and no aggenital setae. In the Borneo material, setae *ad*₁ appear to be relatively shorter.

On the infracapitulum, the genal setae *a* are much thicker than *m* and *h* and there are two pairs of adoral setae. In the typical subspecies setae *or*₁ are setose while in the Borneo material both the adoral setae are smooth.



FIGS. 55–61. *Microtritia tropica dusan* subsp. nov. 55, Tarsus I. 56, Palp. 57, Bothridium and sensillus. 58, Chela. 59, Paraxial oncofysis of the principal cheliceral segment. 60, Tarsus I, dorsal aspect of proximal region. 61, Egg chorion.

The chelicerae (Text-fig. 58) are 110 μ m in length. Both digits have four teeth and the paraxial onychophysis is smooth. Seta *cha* is short and fine with a large insertion pore, while seta *chb*, which arises from a membranous tubercle on the antiaxial surface, is very much longer. The integument of the principal segment carries only a few spines, about two on the paraxial surface and three on the antiaxial.

The three-segmented palps (Text-fig. 56) have the setal formula (2-1-8) and as in *M. t. tropica* the dorsal seta on the palp femur is shorter than the ventral seta.

Märkel (*op. cit.*) notes that the leg chaetotaxy of *M. tropica* is similar to that of *M. minima* (Berlese). The arrangement of the setae on the legs of the Borneo material also agrees well with that of *M. minima*, although there are minor differences. For example, in Märkel's figure of tarsus I of *M. minima* seta *ft* is distinctly proximal in relation to the famulus, while in the Borneo material this seta is inserted at the same level as, if not slightly distal to, the famulus (Text-fig. 55).

A single egg in which the chorion was sculptured with a tessellated pattern (Text-fig. 61) was present in one of the Borneo specimens.

MATERIAL: Holotype female, B.M.(N.H.) Reg. No. 1968 : 738 and two paratypes (both females), B.M.(N.H.) Reg. No. 1968 : 739-740, from sample B124.

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FRANCIS WINSTON EDRIC ROWE

Xref

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A REVIEW OF THE FAMILY HOLOTHURIIDAE (HOLOTHURIOIDEA: ASPIDOCHIROTIDA)

By F. W. E. ROWE

SYNOPSIS

Since the attempts of Pearson (1914) and Panning (1929-35) to revise or subdivide the genus *Holothuria* Linnaeus, 1767 in order to try and show natural affinities between the included species, Deichmann (1958) has been the only specialist in this field to attempt such a task. None of these specialists was able to make a complete survey due to lack of material of certain species.

On the basis of the holothurian collections of the British Museum and the existing literature, an attempt is made in this paper to deal with the balance of those species not taken into consideration by Deichmann and to bring her system into line with the Rules of Nomenclature.

Excluding those of *Actinopyga*, *Bohadschia* and *Labiodemas*, the number of species of *Holothuria* considered to be valid at present is about 114. These can be grouped into 17 more or less clearly distinct supraspecific taxa, four of them new, of varying degrees of differentiation. Some of these groups can be arranged in sequence using the complexity of the spicules as a major criterion.

HISTORICAL INTRODUCTION

UNTIL recently six nominal genera of Holothuriids have been commonly accepted, these being *Holothuria* Linnaeus, 1767, *Actinopyga* Bronn, 1860 (a replacement name for *Muelleria* Jaeger, 1833, pre-occupied), *Bohadschia* Jaeger, 1833, *Microthele* Brandt, 1835, *Labiodemas* Selenka, 1867 and *Halodeima* Pearson, 1914. The last five have been treated as being of subgeneric rank by some authors.

In 1924 (Opinion 80) the generic name *Holothuria* Linnaeus, 1767, as restricted by Brugière, 1791, with type-species *H. tremula* Linnaeus, 1767 (non Gunnerus, 1767) = *H. tubulosa* Gmelin, 1790, was placed on the Official List of Generic Names in Zoology. This action therefore firmly established the generic name *Holothuria* in the present sense rather than the original one of Linnaeus, 1758, when it included only species other than Echinoderms.

This validation was evidently overlooked by Deichmann (1958), who considered that the name *Holothuria* Linnaeus (i.e. sensu 1758) would be better discarded and the species previously included in it divided up into a number of separate genera. She accordingly put forward 13 generic names of which 11 were new to science. Although in doing this Deichmann has disregarded a number of appropriate prior genus-group names of Brandt (1835), Jaeger (1833), Haacke (1880) and Pearson (1914) on the grounds of poor definition, most of these names *are* available under the Rules, being associated with recognized species, those of Jaeger and Brandt needing only designations of type-species in order to qualify for recognition under the Rules.

Despite her non-conformity, Deichmann's revision is of considerable importance in the field of holothurian taxonomy, since it reduces the unwieldy mass of species formerly included in *Holothuria* into more manageable groups within which there

appears to be greater affinity. However, Deichmann was dealing predominantly with species of the East Pacific area and left unconsidered a number of others from different parts of the world, so that her revision was necessarily incomplete.

In an attempt to stabilize the nomenclature, a proposal has been submitted to the International Commission of Zoological Nomenclature (A. M. Clark & F. W. E. Rowe, 1967*a*) requesting that certain of Brandt's and Jaeger's names for supraspecific taxa be formally rejected by use of the plenary powers, or else be reduced to synonymy by selection of appropriate type-species. However, we considered that there is no case for ignoring the priority of both *Cystipus* Haacke, 1880 and *Thymiosicya* Pearson, 1914, of which *Fossothuria* and *Brandtothuria* both of Deichmann, 1958, are respectively junior synonyms.

Deichmann (1958) designated *Holothuria sanctori* Delle Chiaje as type-species of Brandt's *Microthele*. This is inadmissible since *sanctori* was not among the species listed by Brandt. Accordingly we designated *H. (Microthele) maculata* Brandt as type-species, for which the proper name is *H. (Microthele) nobilis* (Selenka) since *maculata* Brandt is a junior homonym.

The group of species included by Deichmann under the name *Microthele* is not consubgeneric with *nobilis* and must therefore be found a new genus-group name.

The intricacies of the nomenclatorial problems which have arisen from Deichmann's work are dealt with in the submission to the International Commission. However, in this paper I give a full list of the supraspecific taxa represented in the family Holothuriidae together with a diagnosis and a list of species referable to each, besides a key to these supraspecific taxa. The figures given in the text are original with the exception of Text-fig. 11; where practicable these have been taken from type-species.

CLASSIFICATION

The identification of all genera and species of holothurians depends almost entirely on the form and combinations of the calcareous spicules found in the body wall and podia. These are commonly subdivided into three-dimensional ones (i.e. tables) near the surface and two-dimensional ones (e.g. buttons; rods) deeper in the body wall, though in some taxa (e.g. *Actinopyga*, *Bohadschia*, *Selenkothuria*) the necessity for roughening the surface seems to be absent and only one kind of spicule—two-dimensional branched rods or flat plates—is present.

The form of the calcareous ring and the arrangement of the tube feet also provide useful taxonomic characters. A similar conclusion, for the Dendrochirotrida at least, has been reached by Pawson & Fell (1965). Other anatomical characters such as the number and arrangement of the tentacles, the presence or absence of anal 'teeth' or papillae, polian vesicles, stone canals and cuvierian organs are variable to some extent even within species and therefore can rarely be used satisfactorily in classification.

DISCUSSION

Previous studies of spicules, confirmed by my own observations, have shown that spicule complexity forms a sound basis for recognizing groups of species within *Holothuria* sensu extenso. This was done by Pearson (1914) who divided *Holothuria*

into five subgenera *Bohadschia* Jaeger, *Actinopyga* Bronn and three new subgenera *Argiodia*, *Halodeima* and *Thymiosycia*. He believed that by elaboration of the simple branched rods and rosettes of the species of *Actinopyga* and *Bohadschia*, perforated plates and later buttons and tables could have developed. He substantiated his conclusion by considering that the form of the calcareous ring in *Actinopyga* and *Bohadschia*, lacking anterior and posterior projections and having deep ampullary notches (shown as deep scallops on the anterior margin of the ring), is primitive in comparison with the form of the calcareous ring in *Argiodia*, *Halodeima* and *Thymiosycia* which shows marked anterior projections of the radial and inter-radial plates, the projections being clearly separated by a deep indentation; the radial plates are also markedly longer than the interradianal plates. Although he laid little store on the taxonomic value of the presence or absence of anal 'teeth' or papillae, Pearson did consider that the arrangement of the tube feet also gives support to his theory that *Actinopyga* and *Bohadschia* are more primitive than his three new subgenera. Pearson dealt only with a few species from the Indian Ocean, so his revision was incomplete.

Panning (1929-35), in his revision of *Holothuria*, recognized *Actinopyga* and *Bohadschia* with *Microthele* as subgenera and arranged the remaining 113 species which he recognized in small rather ill-defined and nameless groups within *Holothuria* sensu stricto. This arrangement was due, notes Deichmann (1958), to 'his dependence in too many cases on the accounts of earlier writers; hence' she says 'many errors have been perpetuated and related forms have been placed far apart'. Later (1939) Panning revised his treatment of *Holothuria*. He was unsure of the relationships between *Actinopyga* and *Bohadschia* since he did not consider the presence or absence of anal papillae as of great importance, but concluded that there could be no close relationship between *Actinopyga* and *Microthele*, the possession of anal papillae in both being the result of a convergence; accordingly he raised all three to generic rank. He also considered that the formation of ellipsoidal bodies found in *Holothuria arguinensis* and *H. mammata* is again a convergence attributable in this case to geographical affinity, the bodies of the former being formed from rosettes and of the latter from buttons. Simultaneously he revised his earlier view that rosettes, as found in *H. edulis* and *H. poli*, are a modified form of button. This presumably followed his studies of the optical properties of various spicules between 1928 and 1935 in which field one of the leaders was Schmidt (1925, 1930) who had concluded that the spicules of holothurians, like the plates of other echinoderms, consist of a single crystal of calcite and that the position of the optical axis of this crystal is of taxonomic importance.

However, Hampton (1958) in making a chemical analysis of the spicules of a single specimen of *Holothuria impatiens* suggested that variations in the optical axis might be due to the differing concentrations of Magnesium present in the spicules, a feature correlated with differences in the temperature of the sea water. He concluded that if this were so then the position of the axis is only of importance as an ecological rather than a taxonomic factor. Clearly further research into the optical properties of spicules must be carried out before their true value in the taxonomy of holothurians can properly be assessed.

Deichmann (1958) draws (though not directly) a correlation between ecology and the form of the spicules. In her revision of *Holothuria* there appear to be three main ecological divisions:

a. Surf-zone species found clinging to rocks. These have terminally-placed bushy tentacles which Deichmann considers may function in the capture of planktonic food; the external layer of tables is usually totally absent, the spicules being represented by rods or plates. These are referable to the taxon *Selenkothuria*, notably *H. (Selenkothuria) lubrica*, *H. (S.) glaberrima* and *H. (S.) moebii*.

b. Fugitive species, i.e. those found usually partly concealed under coral fragments, sand, rocks etc. These have terminally- or ventrally-placed peltate tentacles; their spicules comprise tables in combination with either buttons, rods, rosettes or pseudo-buttons but the two-dimensional spicules are usually smooth structures not possessing knobs. These are referable to the taxa *Thymiosycia* Pearson (including *Brandtothuria* Deichmann) notably *H. (Thymiosycia) impatiens* and *H. (T.) arenicola*; *Lessonothuria* notably *H. (Lessonothuria) pardalis*; *Mertensiothuria* notably *H. (Mertensiothuria) leucospilota*; *Semperothuria* notably *H. (Semperothuria) languens*; *Irenothuria* notably *H. (Irenothuria) maccullochi*; *Vaneyothuria* notably *H. (Vaneyothuria) lentiginosa*; *Halodeima* Pearson (including *Ludwigothuria* Deichmann) notably *H. (Halodeima) atra* and a new taxon in place of *Microthele* sensu Deichmann non Brandt, with type-species *Holothuria difficilis* Semper.

c. Fossorial species, i.e. those capable of burrowing or digging, found buried more or less completely in the substrate. These have relatively small, terminally- or ventrally-placed, peltate tentacles; their spicules comprise knobbed buttons and tables, either kind of spicule becoming elaborated into fenestrated ellipsoidal or spherical bodies. These are referable to the taxa *Cystipus* Haacke (including *Fossothuria* Deichmann and *Jaegerothuria* Deichmann) notably *H. (Cystipus) rigida* and *H. (C.) inhabilis*; also *Theelothuria* notably *H. (Theelothuria) princeps*.

As a summary of Deichmann's work I give here a table of the supraspecific taxa with their type-species represented in her paper together with their present disposition. This is followed by a complementary list of the new taxa described here.

GENUS-GROUP NAME	TYPE SPECIES	PRESENT DISPOSITION
<i>Labidodemas</i> Selenka, 1867	<i>L. semperianum</i> Selenka, 1867	Valid genus
<i>Microthele</i> : Deichmann, 1958 (non Brandt, 1835)	<i>Holothuria sanctori</i> Delle Chiaje, 1823	<i>Holothuria (Platyperona)</i> subg. nov.; type-species <i>Holothuria</i> <i>difficilis</i> Semper, 1868
<i>Brandtothuria</i> Deichmann, 1958	<i>H. arenicola</i> Semper, 1868	<i>H. (Thymiosycia)</i> Pearson, 1914; type species <i>Fistularia impa-</i> <i>tiens</i> Forskaal, 1775
<i>Lessonothuria</i> Deichmann, 1958	<i>H. pardalis</i> Selenka, 1867	Valid subgenus
<i>Mertensiothuria</i> Deichmann, 1958	<i>Stichopus leucospilota</i> Brandt, 1835	Valid subgenus
<i>Semperothuria</i> Deichmann, 1958	<i>Holothuria languens</i> Selenka, 1867	Valid subgenus
<i>Irenothuria</i> Deichmann, 1958	<i>I. maccullochi</i> Deichmann, 1958	Valid subgenus

<i>Vaneyothuria</i> Deichmann, 1958	<i>Holothuria lentiginosa</i> v. Marenzeller, 1893	Valid subgenus
<i>Ludwigothuria</i> Deichmann, 1958	<i>H. atra</i> Jaeger, 1833	<i>Holothuria (Halodeima)</i> Pearson, 1914; type-species <i>H. atra</i> Jaeger, 1833
<i>Selenkothuria</i> Deichmann, 1958	<i>H. lubrica</i> Selenka, 1867	Valid subgenus
<i>Fossothuria</i> Deichmann, 1958	<i>Stichopus rigidus</i> Selenka, 1867	<i>H. (Cystipus)</i> Haacke, 1880; type- species <i>C. pleuripus</i> Haacke, 1888, a junior subjective syn- onym of <i>rigidus</i> Selenka, 1867
<i>Jaegerothuria</i> Deichmann 1958	<i>Holothuria inhabilis</i> Selenka, 1867	<i>H. (Cystipus)</i> Haacke, 1880
<i>Theelothuria</i> Deichmann, 1958	<i>H. princeps</i> Selenka, 1867	Valid subgenus

NEW TAXA:

TYPE-SPECIES DESIGNATED HERE

<i>Acanthotrapeza</i> subg. nov.	.	.	.	.	<i>Holothuria pyxis</i> Selenka, 1867
<i>Metriatyla</i> subg. nov.	.	.	.	.	<i>H. scabra</i> Jaeger, 1833
<i>Panningothuria</i> subg. nov.	.	.	.	.	<i>H. forskali</i> Delle Chiaje, 1823
<i>Platyperona</i> subg. nov.	.	.	.	.	<i>H. difficilis</i> Semper, 1868
<i>Stauropora</i> subg. nov.	.	.	.	.	<i>H. discrepans</i> Semper, 1868

Deichmann considered that of the species which have been included in *Holothuria*, excluding *Actinopyga* and *Bohadschia*, 'the most primitive are undoubtedly those with numerous, regular tables and smooth, regular buttons' she continues 'a more advanced stage is indicated by the presence of irregular buttons or development of rosettes or reduction of the inner layer of spicules while the tables have become variously modified'. This implies that the rosettes to be found in certain species have developed as a result of reduction of buttons rather than an advancement on branched rods as Pearson considered. It further implies, if this concept is correlated with Deichmann's ecological divisions, that the role of the tables or other three-dimensional spicules is to provide a roughened body surface to give frictional support to the fossorial species, the degree of roughness or complexity of the spicules being related to the degree to which the species is fossorial. Conversely, in the species of *Holothuria (Selenkothuria)* (that is surf-zone species found in more exposed places such as rock crevices, and presumably not at all fossorial in habit) frictional support is not important and the outer layer of tables is lacking leaving only plates and rods, though these may be rather spinose but in a single plane. This may also account for the simplification of the spicules in the species of *H. (Mertensiothuria)*, *H. (Irenothuria)*, *H. (Holothuria)*, *H. (Stauropora)* and *H. (Panningothuria)* with fugitive but not necessarily fossorial habits.

With regard to the fossorial habits of Aspidochirotcs I can trace no studies of the role of the podia in burrowing. The extent of crowding of the locomotory podia (pedicels) on the rather flattened ventral surface and the specialization of wart-like sensory podia (papillae) on the arched dorsal surface contrasts markedly with the arrangement in such fossorial genera and species as the dendrochirots *Echinocumis* and *Thyone* with unmodified podia scattered all over the body surface, the

species apparently 'ploughing into the substrate dorsal side up through alternate circular and longitudinal contractions until the middle region is buried' according to Hyman (1955). This process is facilitated by the attachment of the podia to any solid objects. The arrangement of the podia of *Aspidochirotetes* therefore suggests that they are not active burrowers but are capable only of pushing into or under loose sand, fragmentary substrates or boulders and rocks, this being aided by the frictional support afforded to the bodywall by the spicules. The degree to which the species are fossorial is probably directly proportional to the degree of complexity of the spicules they possess.

It must be mentioned that the fossil history of holothurians is little known. However, according to Pawson (1966) the earliest holothurians are believed to be extensively plated forms in line with other members of the Echinozoa, the most primitive extant genus being *Placothuria* Pawson & Fell 1965 (a dendrochirote). Unfortunately Pawson only deals in detail with the *Dendrochirotida* briefly mentioning that 'no special attention has been directed towards the other holothurian assemblages'.

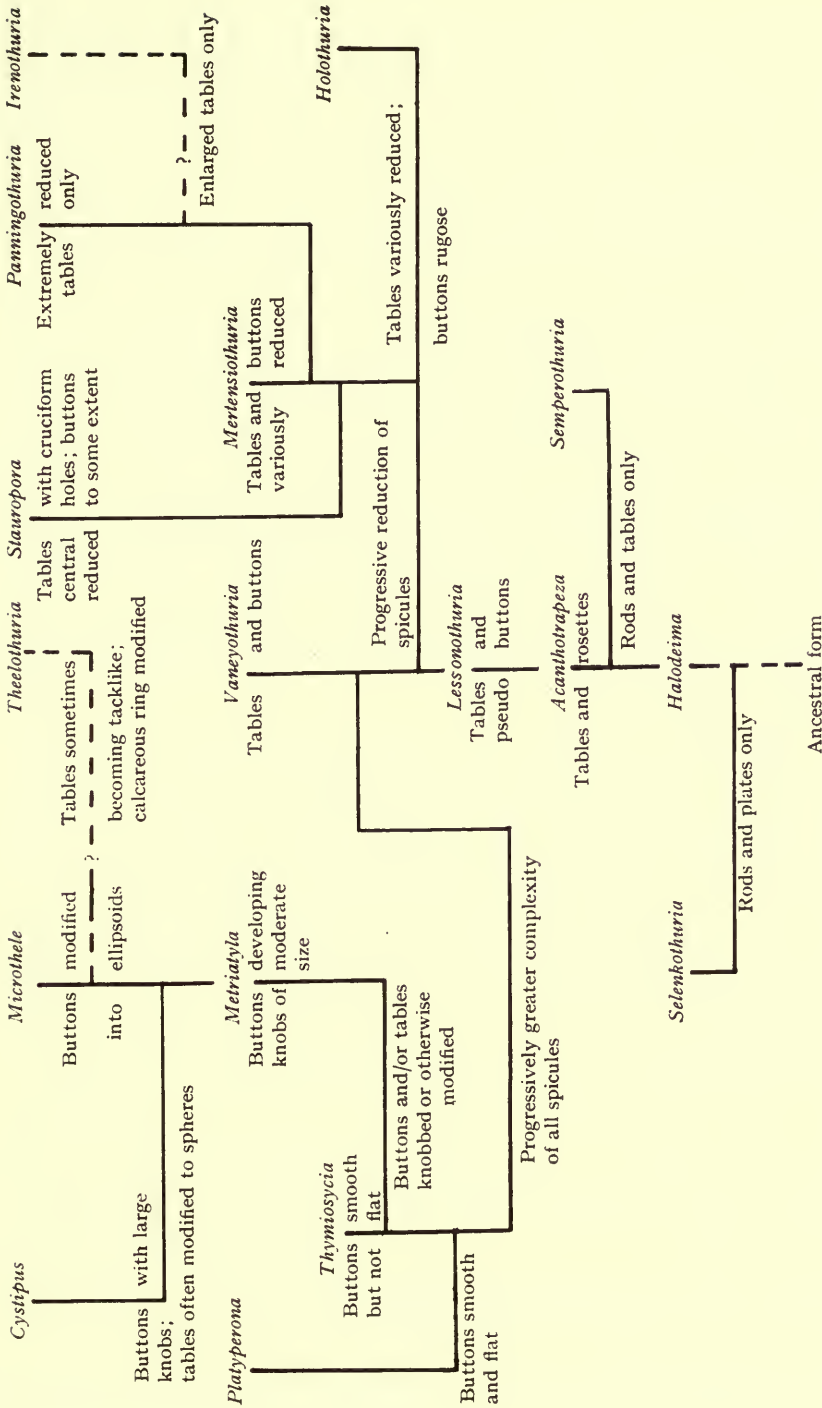
Contrary therefore to Deichmann's conclusions, it seems to me more likely that the fossorial habit, correlated with multiplicity of spicule form and with compact aspidochirotid peltate tentacles adapted to sweeping the substrate en masse into the mouth, evolved from the exposed rock-clinging habit correlated with simplicity of spicule form and with arborescent tentacles adapted for suspension feeding. The taxon *Selenkothuria* with only plate-like spicules¹ together with tentacles of the more arborescent form, approximating to that of the suspension-feeding dendrochirotidids of non fossorial or fugitive habit, may therefore represent the primitive condition. This line of reasoning follows closely the implication by Pawson (1966) that the extensively-plated dendrochirotes are probably the most primitive holothurians. The direction of evolution within the holothuriids is still not clear, however, so it may be that the condition in *Selenkothuria* represents a secondary reversion.

It seems to me worthwhile to draw up a hypothetical evolutionary tree for the holothuriid taxa (Text-fig. 1) based on spicule complexity. The speculations involved here should at least form a basis for future argument.

Clearly before the full significance of spicule form as an indicator of affinity between the groups of species can be recognized much more field work is needed on their ecology. This is especially the case since many taxa now established are subsequent to Deichmann's work and their ecology has not yet been sufficiently correlated with her rather neat conception of the ecology and taxa of Eastern Pacific species, a project I am unfortunately not in a position to complete. The optical properties of spicules and their changes during ontogeny also need further study since it is well known that in the few species studied the spicules of juvenile, adult and sometimes senescent specimens often differ considerably. It is not known how long-lived the individual spicules are; whether they are replaced or modified with age.

As for the rank which should be accorded to Deichmann's taxonomic groups of *Holothuria* sensu extenso and the new ones added here, having regard to the evidence

¹ Rudimentary tables are said to occur in a few species such as *H. (Selenkothuria) moebii* and *erinaceus* although I could not find any in the few specimens available.


 FIG. 1. Provisional hypothetical evolutionary tree of the subgenera of *Holothuria*. (see also table on p. 165).

already outlined, the varying degrees of differentiation between the groups of species and the present climate of opinion, I believe that a conservative attitude is the best one to adopt and therefore consider that they should be regarded as *subgenera* rather than *genera* as Deichmann (1958) treated them. Since Deichmann's division of *Holothuria* only Tikasingh (1963) in his first paper on holothurians, and clearly on Deichmann's advice, has completely adopted her division at generic level. Caso (1963, 1964 and 1965), though distinguishing two new taxa *Holothuria* (*Paraholothuria*) (1963) and *Microthele* (*Paramicrothele*) (1964), recognized (in 1965), only *Irenothuria* Deichmann, as a distinct genus referring other Mexican species back to *Holothuria*.

To my knowledge no other specialists have yet cared to commit themselves one way or the other with regard to Deichmann's division of *Holothuria*.

The body form, spicules and calcareous ring of the species of *Actinopyga* and *Bohadschia* appear to me incompatible with those of the remainder of species under consideration, accordingly no attempt is made here to treat them as anything other than valid genera. Also I have continued so to treat *Labidodemas*, distinguished by its cylindrical body form with podia restricted to the ambulacra and by its calcareous ring. The only similarity to *Holothuria* it bears is in possessing tables and sometimes buttons as spicules. In truth I think *Labidodemas* may even prove to warrant separation at family level.

The following key to the supra-specific taxa of the family Holothuriidae should serve to place species of unknown position.

- 1 Spicules: very numerous branched rods, usually dichotomously lobed; tables, buttons, rosettes, perforated plates *never* present 2
 - 1' Spicules: tables of some form nearly always present; buttons, rods, rosettes, perforated plates present or absent; dichotomously lobed rods, if present, then only in combination with tables, *never* on their own. 3
- 2 Anus guarded by five enlarged calcified papillae or anal 'teeth'
 - 2' Anus not guarded by five enlarged calcified papillae though five groups of smaller papillae may be present genus **ACTINOPYGA** Bronn, 1860
 - 3 Calcareous ring slender and ribbon-like with radial plates shorter than wide and interradial plates likewise, the latter tending to be curved; podia restricted to the ambulacral areas genus **BOHADSCHIA** Jaeger, 1833
 - 3' Calcareous ring more or less stout, not ribbon-like, radial plates as long as or longer than wide, interradials about half as long as wide but not so wide as to be curved; podia in the form of locomotory pedicels on the ventral surface which is often flattened, and more or less sensory conical papillae on the dorsal surface which is often arched genus **LABIDODEMAS** Selenka, 1867
- 4 Spicules: perforated or thorny rods or plates, tables said to be present in some species but if so always reduced in form and sparsely distributed in the body wall
 - 4' Spicules: tables always present, usually well developed, alone or in combination with buttons, pseudobuttons, rods or rosettes 5
- 5 Spicules: tables always present in combination with rods or rosettes, never with buttons or pseudobuttons 6
 - 5' Spicules: tables always present in combination with buttons or pseudobuttons, no rosettes or rods 8

H. (*Selenkothuria*) Deichmann, 1958

- 6 Spicules: tables present in combination with rosettes; no rods in the body wall 7
6' Spicules: tables present in combination with rods in the body wall, tables usually with reduced disc and spire of moderate height¹, either rounded at the tip or terminating in a few spines which form a single or double maltese cross when viewed from above; no rosettes **H. (Semperothuria)** Deichmann, 1958

7 Spicules: tables usually with reduced disc and moderately high or high spire, ending in a few spines forming a maltese cross when viewed from above
. **H. (Halodeima)** Pearson 1914
7' Spicules: tables large and clumsy with spinose well-developed disc, its rim is often turned up to give a 'cup and saucer' appearance to the table in lateral view, spire of low to moderate height **H. (Acanthotrabeza)** subg. nov.

8 Spicules: tables always present, with low, moderate or high spire terminating in a ring or cluster of small spines, disc usually squarish or octagonal with a large centrally-placed cruciform hole, one or more smaller holes alternating with each arm of the central cross giving the disc a very characteristic appearance, the rim of the disc smooth or spinose, flat or slightly turned up to give the table a 'cup and saucer' aspect in lateral view; buttons usually present, rarely totally absent, very variable, oval, smooth or rugose, occasionally incomplete or even reduced to small bars with lateral lobes, complete buttons usually with three to six pairs of holes **H. (Stauropora)** subg. nov.

8' Spicules: tables always present, variously developed, never with the central hole of the disc cruciform in shape; buttons variously developed or totally absent, rosettes sometimes present 9

9 Spicules: tables present alone, buttons totally absent. 10
9' Spicules: tables variously developed, buttons always present. 11

10 Spicules: tables always very reduced, rarely absent (probably only in badly preserved specimens), disc ovoid, usually with two to four holes, spire reduced to one to four knobs or short spines. **H. (Panningothuria)** subg. nov.

10' Spicules: tables with well developed multilocular disc and tall spire with a crossbeam near the base and four long smooth pillars diverging at the tip, each tapering to a point, smaller tables also present with shorter spire often reduced to one to four knobs or completely lacking **H. (Irenothuria)** Deichmann, 1958

11 Spicules: tables variously developed, never modified into hollow fenestrated spheres; buttons smooth, regularly or irregularly developed, often twisted. 12
11' Spicules: tables always strongly developed, sometimes modified into hollow fenestrated spheres; buttons always knobbed or rugose or modified to form hollow fenestrated ellipsoids 16

12 Spicules: tables usually well developed, the rim of disc not spinose; buttons not twisted, sometimes flat and thin, with or without an apparent median longitudinal ridge, outline regular or irregular 13
12' Spicules: tables more or less well developed, disc usually spinose; buttons irregular or twisted, never flattened, lacking any appearance of a median longitudinal ridge 14

13 Spicules: tables well developed, disc smooth and round usually with ten or more peripheral holes, spire of moderate height ending in several small spines; buttons oval, thin, flat, very rarely with a few knobs, an apparent median longitudinal ridge present, three to six pairs of relatively small holes, buttons regular or irregular in outline **H. (Platyperona)** subg. nov.

13' Spicules: tables fairly stout, disc smooth, squarish in outline, usually with eight regular peripheral holes, spire of moderate height ending in a cluster of small spines; buttons not thin or flat and lacking any appearance of having a

¹ If the height of the spire is measured against the diameter of the disc then low = < disc diameter, moderate = disc diameter, high = > disc diameter.

- median longitudinal ridge, usually with three pairs of comparatively large holes, and regular in outline **H. (*Thymiosyca*)** Pearson, 1914
- 14 Spicules: tables not strongly developed, rim of disc usually spinose, spire low, ending usually in a ring of spines or cluster of spines, tables occasionally degenerate or incomplete; buttons irregular though not twisted, usually with three pairs of holes, or else incomplete forming small lobed rosette-like bars **H. (*Mertensiothuria*)** Deichmann, 1958
- 14' Spicules: tables always well developed, rim of disc spinose and either flat or turned up to give a 'cup and saucer' aspect to the table in lateral view, spire of low to moderate height; buttons often incomplete, twisted or in the form of pseudobuttons 15
- 15 Spicules: tables clumsy, disc well developed, rim spinose, often turned up to give a 'cup and saucer' aspect to the table in lateral view, spire low to moderate in height, usually terminating in a ring or cluster of small spines; pseudobuttons abundant, smooth, usually irregular and often reduced to a single row of three or four holes, occasionally buttons quite regular with three pairs of holes. **H. (*Lessonothuria*)** Deichmann, 1958
- 15' Spicules: tables not clumsy but well developed, rim of disc spinose but flat, not turned up, spire of moderate height, terminating in several short spines which give the appearance of a maltese cross when viewed from above; buttons usually scarce, smooth, with three to five pairs of holes, often incomplete, sometimes twisted and irregular **H. (*Vaneyothuria*)** Deichmann, 1958
- 16 Spicules: tables always simple and irregular with rather spinose disc which may be somewhat reduced, spire low, moderate or high; buttons simple, quite large, always with numerous small rounded or pointed knobs giving the button a rugose appearance, three to ten pairs of holes which sometimes become obliterated by the thickening of the button **H. (*Holothuria*)** Linnaeus, 1767
- 16' Spicules: tables either modified into fenestrated spheres or more often simple and well developed, disc smooth or spinose or knobbed, spire low to high, buttons with large or moderate-sized knobs, never with numerous small knobs giving the button a rugose appearance, either simple or modified into hollow fenestrated ellipsoids 17
- 17 Spicules: tables with disc usually knobbed, spire low, bearing many short spines which are sometimes so numerous and closely crowded that they may almost either obscure the disc or become connected to the knobs of the margin of the disc thus forming a fenestrated sphere; buttons usually simple with large regularly or irregularly arranged knobs, generally three to four or more pairs of relatively small holes which may become somewhat obscured by the size of the large knobs. **H. (*Cystipus*)** Haacke, 1880
- 17' Spicules: tables stout, well developed, spire moderate or high, never modified into hollow fenestrated spheres; buttons either simple with irregular knobs of moderate size or modified into hollow fenestrated ellipsoids 18
- 18 Spicules: tables well developed, disc smooth or spinose, spires either moderate or high, usually terminating in a cluster of small spines, tables with spires perfectly smooth and tapering to a point giving the whole table a tack-like appearance usually also present; buttons either simple with irregular, moderate-sized knobs, or modified into hollow fenestrated ellipsoids; calcareous ring with radial plates usually possessing more or less well developed posterior bifurcate prolongations. **H. (*Theelothuria*)** Deichmann, 1958
- 18' Spicules: tables well developed, disc smooth, often squarish in outline, spire of moderate height or high, terminating in small spines, never pointed and tack-like; buttons simple with moderate-sized knobs or modified into hollow fenestrated ellipsoids; calcareous ring never with any indication of posterior bifurcate prolongations on the radial plates 19

- 19 Spicules: tables well developed with smooth disc, spire of moderate height or high, terminating in several small spines; buttons simple, with moderate-sized irregularly arranged knobs and three to six pairs of relatively large holes, buttons never modified into hollow fenestrated ellipsoids . . . *H. (Metriatyla)* subg. nov.
- 19' Spicules: tables as for 19; buttons hollow fenestrated ellipsoids though a few simple knobbed buttons may be present . . . *H. (Microthele)* Brandt, 1835

Genus *BOHADSCHIA* Jaeger, 1833

(Text-fig. 2)

Bohadschia Jaeger, 1833 : 18; Panning, 1944 : 35; Cherbonnier, 1955 : 132; A. M. Clark & F. W. E. Rowe, 1967a : 101. (Type-species *B. marmorata* Jaeger, 1833; designated by Pearson, 1914 : 164).

Sporadipus (*Colpochirotia*) Brandt, 1835 : 46. (Type-species *S. (C.) ualanensis* Brandt, 1835, by monotypy; a synonym of *B. marmorata* Jaeger, 1833; see A. M. Clark & F. W. E. Rowe, 1967a : 98-99).

Holothuria (*Bohadschia*) Pearson, 1914 : 169; Panning, 1929 : 120.

DIAGNOSIS: Tentacles 20; pedicels usually scattered but sometimes arranged in three rows on the ventral side, papillae or papillae and pedicels scattered on the

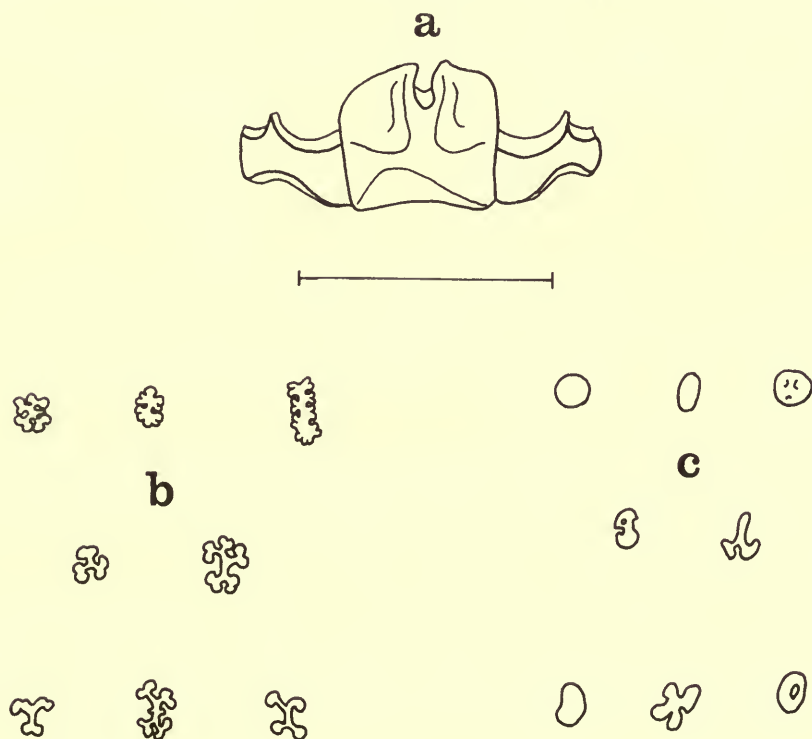


FIG. 2. *Bohadschia marmorata* Jaeger, 1833. B.M. No. 1932.4.28.155, Great Barrier Reef, length 150 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measure 10 mm. for (a) and 0.1 mm. for (b) and (c).

dorsal side; anus sometimes surrounded by five groups of papillae but single calcified anal papillae (anal 'teeth') absent; body wall muscular and thick (with a mean thickness of about 6 mm. and a range of 1-15 mm.; all measurements from preserved specimens); size moderate to large, up to 400 mm. long; calcareous ring strong, well developed with distinctly scalloped anterior margin, the radial plates about twice as big as the interradiial plates and with a median anterior ampullary notch, the interradiial plates with an anterior tooth-like median projection, the union between the plates sometimes imperceptible; spicules consisting of simple grains or short dichotomously branched rods, rarely spinose rods or both, tables and buttons or elaborate plates *never* present.

OTHER SPECIES INCLUDED: *Bohadschia argus* Jaeger, 1833; *Holothuria bivittata* Mitsukuri, 1912; *B. cousteaui*, *B. draschi* Cherbonnier, 1954; *H. graeffei*, *H. koellikeri* Semper, 1868; *H. paradoxa* Selenka, 1867; *H. similis* Semper, 1868; *B. steinitzi* Cherbonnier, 1963; *H. subrubra* Quoy & Gaimard, 1833; *H. tenuissima*, *H. vitiensis* Semper, 1868.

REMARKS: The spicules found in species of the genus *Bohadschia* vary from small oval non-perforated or perforated grains to short, dichotomously-branched rods, with the exceptions of *B. graeffei* (Semper), from the Indo-West Pacific (including the Red Sea), and *B. draschi* Cherbonnier from the Red Sea, which possess in addition, peculiar 'raquet-shaped' spicules. The separation of the species depends generally on the complexity of branching of the rods.

Genus *ACTINOPYGA* Bronn, 1860

(Text-fig. 3)

Muelleria Jaeger, 1833 : 7; Selenka, 1867 : 310; Mitsukuri, 1912 : 43 (Non *Muelleria* Férussac, 1823, Mollusca).

H. (Microthele) (part) Brandt, 1835 : 54.

Actinopyga Bronn, 1860 : 403 (replacement name for *Muelleria* Jaeger, 1833); Deichmann, 1930 : 79; Fisher, 1907 : 644; H. L. Clark, 1921 : 188; Panning, 1944 : 45; Cherbonnier, 1955 : 135; Clark & Rowe, 1967a : 101. (Type-species *Muelleria echinites* Jaeger, 1833; designated by A. M. Clark & F. W. E. Rowe, 1967a : 101).¹

Holothuria (Actinopyga): Pearson, 1914 : 169; Panning, 1929 : 125.

DIAGNOSIS: Tentacles 20-30 (usually 20 or 25); pedicels usually arranged in three more or less distinct rows on the ventral side, papillae only on the dorsal side, scattered; anus with five distinct calcified anal papillae ('teeth'); body wall similar to that found in *Bohadschia*; size as *Bohadschia*; calcareous ring similar to that found in *Bohadschia*; spicules consisting of rods, generally more slender than those of

¹ Bronn (1860) did not designate a type-species for *Actinopyga*, while Pearson (1914) and Panning (1939) both designated *Holothuria miliaris* Quoy and Gaimard, 1833, as type-species. This is invalid since *H. miliaris* was not included by Jaeger (1833) in *Muelleria* (for which *Actinopyga* was a replacement name) [see A. M. Clark & F. W. E. Rowe, 1967a : 101].

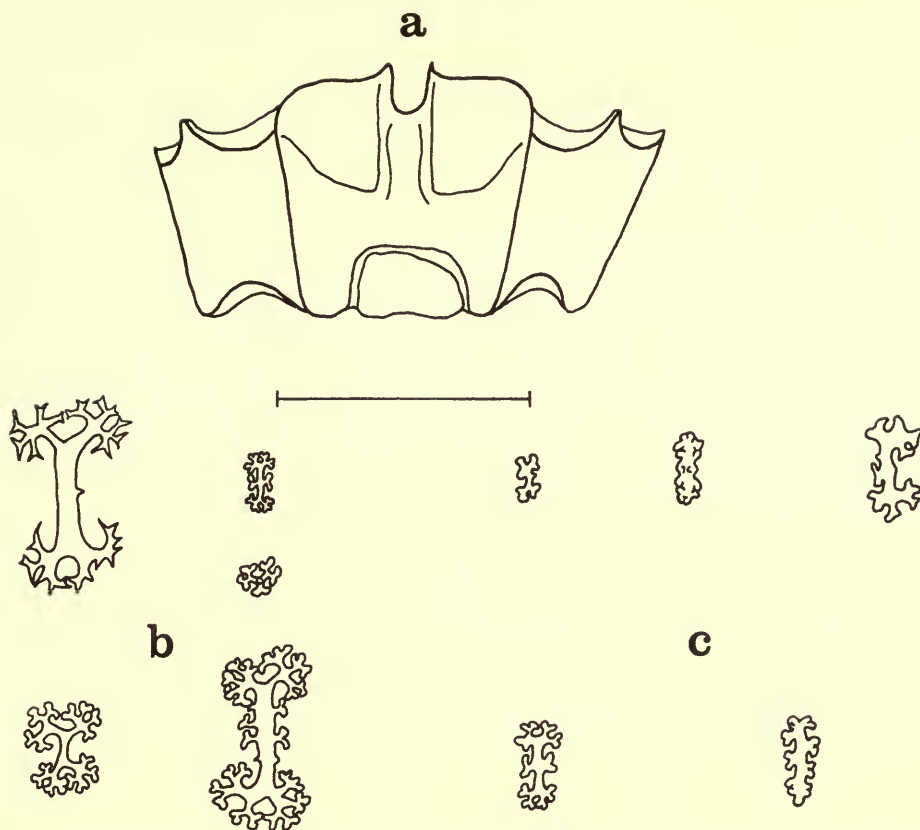


FIG. 3. *Actinopyga echinites* (Jaeger, 1833). B.M. No. 1930.7.30.90, Seychelles, length 150 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0.1 mm. for (b) and (c).

Bohadschia, dichotomously branching not so profuse, spinose rods more commonly present, tables, buttons or elaborate plates *never* present.

OTHER SPECIES INCLUDED: *Muelleria agassizi* Selenka, 1867; *Actinopyga bannwarthi*, *A. crassa* Panning, 1944; *M. lecanora* Jaeger, 1833; *Holothuria mauritiana*, *H. miliaris* Quoy & Gaimard, 1833; *M. obesa* Selenka, 1867; *A. palauensis* Panning, 1944; *M. plebeja*, Selenka, 1867; *A. serratidens*, Pearson, 1905.

REMARKS: The species of *Actinopyga* are separated from each other by the form and complexity of the rods. Small grains like those found in *Bohadschia* are virtually absent and the rods are generally longer, relatively more slender and less profusely branched.

The tentacle number is usually about 20 though *A. agassizi* from the West Indian region and *A. mauritiana* from the Indo-West Pacific have 25–29, being distinguished from each other by the difference in spicule complexity.

Genus *LABIDODEMAS* Selenka, 1867

(Text-fig. 4)

Labidodemas Selenka, 1867 : 309; Semper, 1868; Ludwig, 1875; Sluiter, 1901; H. L. Clark, 1921; Deichmann, 1958. (Type-species *L. semperianum* Selenka, 1867; by monotypy).
Holothuria (part): Ludwig, 1875.

DIAGNOSIS: Tentacles 20; pedicels and papillae generally confined to the ambulacral areas; no apparent anal 'teeth' or papillae; body wall soft or leathery, fairly thick, about 1.5 (1-2) mm.; body cylindrical or vermiform; size moderate, up to 150 mm. long; calcareous ring ribbon-like, radial and interradial plates shorter than broad; spicules usually few, tables scattered, variously developed, either with disc reduced and spire low, ending in a ring of spines or else disc well developed and spinose with spire of moderate height and usually also very spinose, buttons when present smooth, irregular, often incomplete or deformed, suggesting clumsy 'C'-shaped bodies, minute curved rods sometimes present.

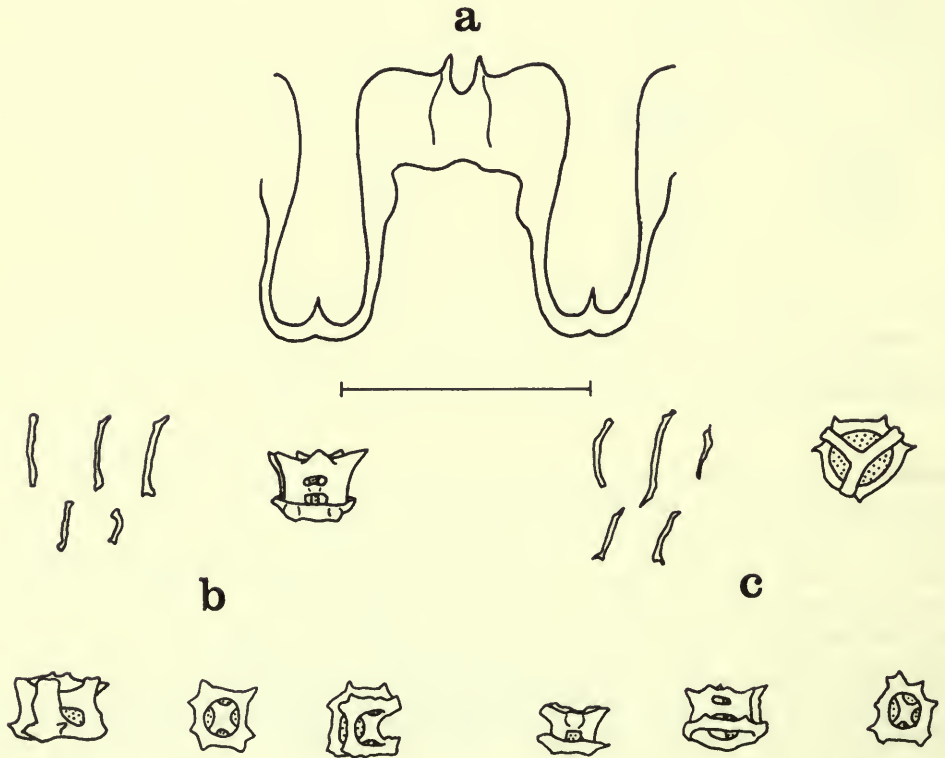


FIG. 4. *Labidodemas semperianum* Selenka, 1867. B.M. No. 1955.10.14.48, Maldives, length 190 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0.1 mm. for (b) and (c).

OTHER SPECIES INCLUDED: *Labidodemas americanum* Deichmann, 1938; *Holothuria rugosa* Ludwig, 1875.

REMARKS: Until now only two species were considered referable to *Labidodemas* these being *L. semperianum* from the Indo-West Pacific region and *L. americanum* from the East Pacific region including the Galapagos Is., according to Deichmann, 1958. However, I have no hesitation in including *Holothuria rugosa*, another Indo-West Pacific species, in the list of species because of its body form and the structure of the calcareous ring. It can be immediately separated from the other two species by the form of its spicules, these being extremely spinose tables with spinose spires of moderate height and smooth irregular buttons. *L. americanum*, which H. L. Clark (1946) considers is possibly not congeneric with *L. semperianum*, has delicate tables with a more or less complete ring of holes to the disc and the spire sometimes reduced, while the type-species has stout tables with long spines on the tip of its low spire and the disc reduced or absent. A few deformed buttons are usually present.

Seven other nominal species have been referred to *Labidodemas*, namely *L. egestosum* Sluiter, 1901, *L. dubiosum* Ludwig, 1875 and *L. selenkianum* Semper, 1868 all of which H. L. Clark (1921) considered to be conspecific with *L. semperianum*. *L. pertinax* (Ludwig), 1875 which Deichmann (1958) considered to be conspecific with *L. semperianum*. *L. leucopus* and *L. neglectum* Haacke, 1880, which Panning (1929-35) considered to be conspecific with *Holothuria monacaria* Lesson (sensu Théel) (= *hilla* Lesson according to Cherbonnier, 1951) and finally *L. punctulatum* Haacke, 1880, which Panning considered to be conspecific with *H. pardalis* Selenka, 1867.

Genus *HOLOTHURIA* Linnaeus 1767

Holothuria Linnaeus, 1767 : 1089; Opinion 80, 1924 : 17; Panning, 1929-35 (non *Holothuria* Linnaeus, 1758 suppressed). (Type-species *H. tremula* Linnaeus, 1767 [non *H. tremula* Gunnerus, 1767] = *H. tubulosa* Gmelin, 1890; validated, Opinion 80, 1924 : 17-18). *Thelenota* Brandt, 1835 : 53 (non *Thelenota*: H. L. Clark, 1921 : 185).

DIAGNOSIS: Tentacles 17-30, usually 20, pedicels and papillae variously arranged on the ventral and dorsal sides respectively; anal papillae variously developed or absent; body wall very variable; body form showing a wide range, vermiform, cylindrical or with ventral side distinctly flattened and 'sole'-like, dorsally arched; size ranging from small to large, even massive, up to 450 (? 600) mm. long; calcareous ring more or less well developed, usually with radial plates two to three times as long as the interradian plates, the anterior margin of the ring rarely scalloped, the posterior margin undulating (except in subgenus *Theelothuria* where the radial plates bifurcate posteriorly); spicules very diverse and variously developed, tables present (except in the subgenus *Selenkothuria* where tables are absent in five species out of seven and in the other two are said to be present but only in very reduced form. In this subgenus the spicules comprise usually elaborate, smooth, perforated rods

and plates or spinose rods), buttons present or absent, rosettes* and small branched rods sometimes also present.

[The sequence of the subgenera following matches that of the key.]

Subgenus **SELENKOTHURIA** Deichmann, 1958

(Text-fig. 5)

Stichopus (part): Selenka, 1867.

Holothuria (part): Selenka, 1867; Semper, 1868; Ludwig, 1883; Krauss *in* Lampert, 1885; Caso, 1954; Deichmann, 1938.

Selenkothuria Deichmann, 1958 : 314 (Type-species *Holothuria lubrica* Selenka, 1867: designated by Deichmann, 1958 : 314); 1963a, Tikasingh, 1963.

DIAGNOSIS: Tentacles 20; pedicels crowded but more or less distinctly arranged in three rows on the ventral 'sole', papillae small, numerous, scattered dorsally; body wall soft, not very thick, about 1 (1-3) mm.; body with flattened ventral 'sole'

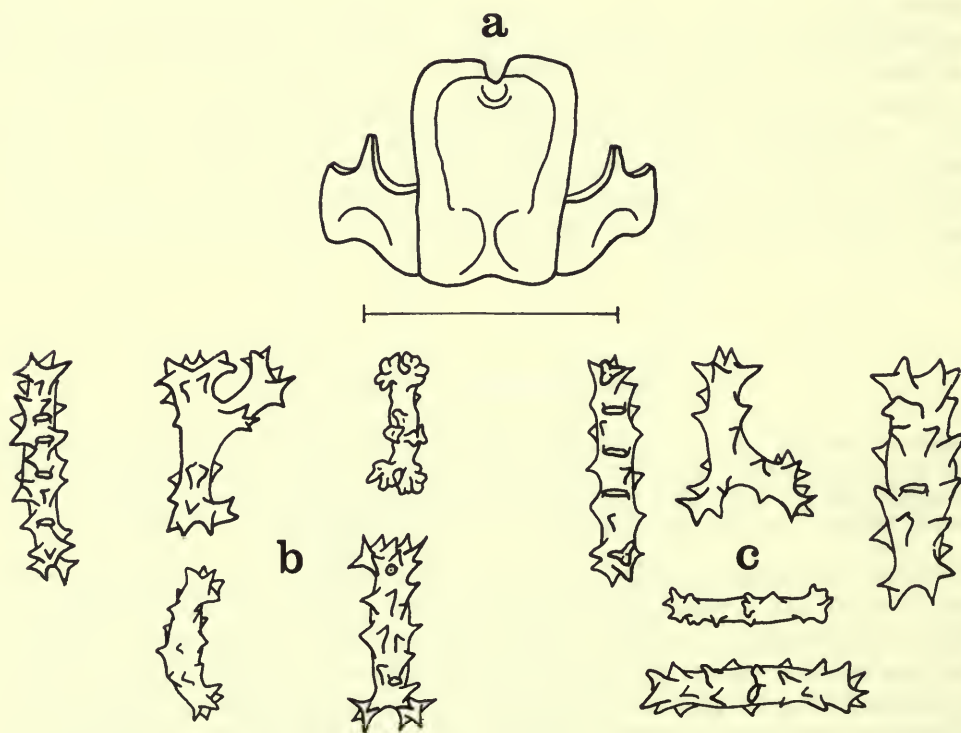


FIG. 5. *Holothuria* (*Selenkothuria*) *lubrica* Selenka, 1867. B.M. No. 1938.12.12.30. 8-10, Ballenas Bay, Costa Rica, length 50 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0.1 mm. for (b) and (c).

* Branched rods whose branches have anastomosed forming a perforated button-like spicule with holes of various sizes usually including median terminal holes.

and arched dorsally; size moderate, up to 150 (rarely 200) mm. long; calcareous ring with radial plates up to three times as long as the interradial plates, the latter usually with the outer surface slightly concave; spicules consisting of perforated or rugose plates or rods, tables rare or more often totally absent, when present (two species) always in very rudimentary form and sparsely distributed in the body wall.

OTHER SPECIES INCLUDED: *Holothuria erinaceus* Semper, 1868; *H. glaberrima* Selenka, 1867; *H. moebii* Ludwig, 1883; *H. parva* Krauss (in Lampert) 1885; *H. portovallartensis* Caso, 1954; *H. theeli* Deichmann, 1938.

REMARKS: The spicules of *Selenkothuria* fall more or less into two categories. Either spinose rods are present, as found in *H. (S.) lubrica* from the eastern Pacific area, *H. (S.) parva* from the western end of the Indian Ocean, *H. (S.) glaberrima* from the West Indies and *H. (S.) moebii* from the Indo-West Pacific region, with rudimentary tables found sometimes in *H. (S.) moebii*, or else flattened plates and rods, as found in *H. (S.) portovallartensis* and *H. (S.) theeli* from the Galapagos and west coast of Mexico, and *H. (S.) erinaceus* from the Indo-West Pacific region, with rudimentary tables present in *H. (S.) erinaceus*.

The species in this subgenus are distinguished from each other most easily by the shape and degree of spinosity of the rods or by the shape and degree of perforation of the flattened plates and rods, an additional factor being the occurrence of tables.

Subgenus **SEMPEROTHURIA** Deichmann, 1958

(Text-fig. 6)

Stichopus (Gymnochirota) Brandt, 1835 : 51 (Type-species *S. (G.) cinerascens* Brandt; designated by A. M. Clark & F. W. E. Rowe 1967a : 101; suppression of subgeneric name simultaneously proposed).

Stichopus (part): Selenka, 1867.

Holothuria (part): Selenka, 1867; Semper, 1868; Ludwig, 1875; Panning, 1929-35.

Semperothuria Deichmann, 1958 : 302 (Type-species *Holothuria languens* Selenka, 1867; designated by Deichmann, 1958 : 303); Tikasingh, 1963.

DIAGNOSIS: Tentacles 20; pedicels more or less distinctly arranged in three rows on the ventral side, papillae scattered dorsally; body wall soft, not very thick, about 2 (1-4) mm.; body rather slender and cylindrical; size moderate, up to 100-150 (rarely 200) mm. long; calcareous ring quite well developed, radial plates up to three times as long as the interradials; spicules consisting of tables in combination with rods, the former with disc reduced or absent, spire high and terminating in a few spines which form a single or double maltese cross when viewed from above, rosettes never present.

OTHER SPECIES INCLUDED: *Stichopus (Gymnochirota) cinerascens* Brandt, 1835; *Holothuria flavomaculata* Semper, 1868; *H. imitans* and *H. surinamensis* Ludwig, 1875.

REMARKS: *Holothuria (Semperothuria) cinerascens* and *H. (S.) flavomaculata* from the Indo-West Pacific region also *H. (S.) surinamensis* from the West Indies

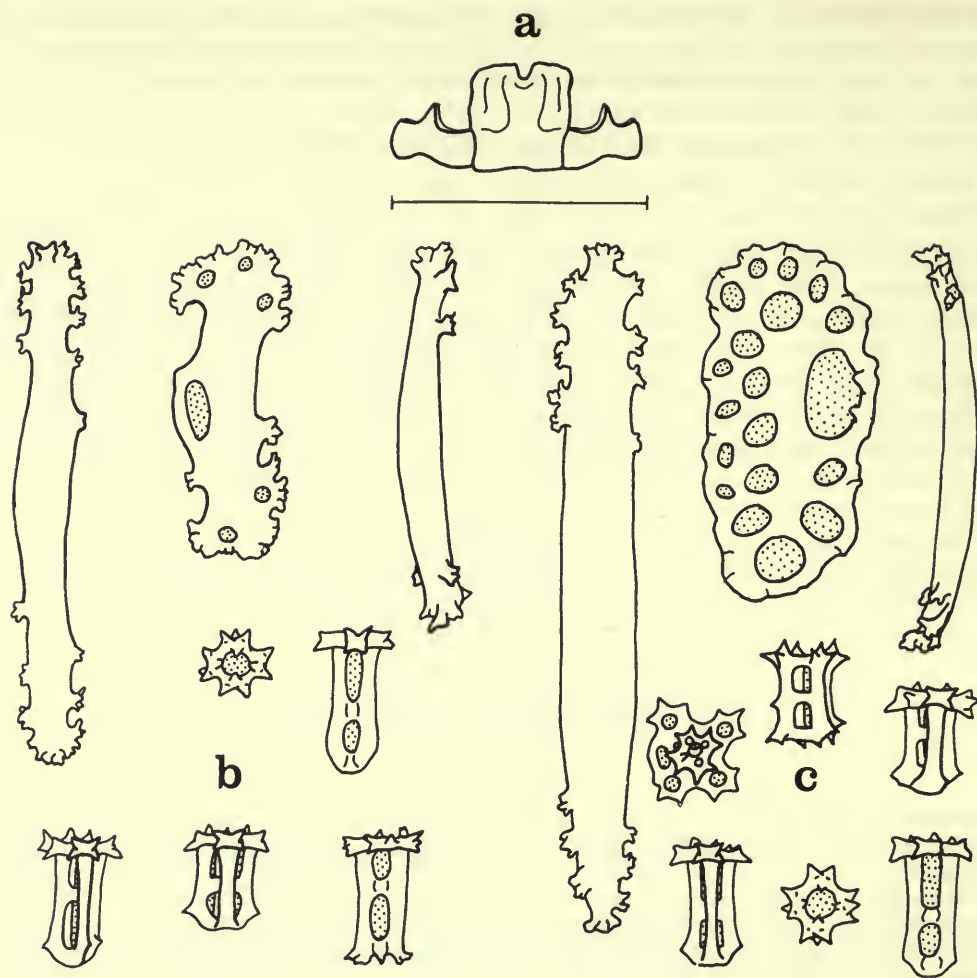


FIG. 6. *Holothuria (Semperothuria) surinamensis* Ludwig, 1875. B.M. No. 1939.2.22.28, South Sound, Cayman Is., West Indies, length 120 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0.1 mm. for (b) and (c).

possess spinose rods, those of *cinerascens* differing from *flavomaculata* and *surinamensis* in being finely spinulose whilst *flavomaculata* and *surinamensis* have rods with fewer but much larger spines. *H. (S.) languens* has, according to Deichmann (1958), flattened smooth rods, the rods usually having a marginal row of holes. The circumtropical species *H. (S.) imitans* appears to lack rods in the body wall, possessing tables and only the supporting rods of the podia.

Subgenus *HALODEIMA* Pearson, 1914

(Text-fig. 7)

Trepang Jaeger, 1833 : 24 (Type-species: *Holothuria edulis* Lesson, 1830; designated by H. L. Clark, 1921 : 184); A. M. Clark & F. W. E. Rowe, 1967a : 100 (proposed suppression). *Holothuria* (part): Lesson, 1830; Jaeger, 1833; Pourtalés, 1851; Selenka, 1867; Semper, 1868; Ludwig, 1875.

Stichopus (part): Selenka, 1867.

Holothuria (*Halodeima*) Pearson, 1914 : 170 (Type-species *Holothuria atra* Jaeger, 1833; designated by Pearson, 1914 : 171).

H. (*Holothuria*) (part): Panning, 1929-35.

Ludwigothuria Deichmann, 1958 (Type-species *H. atra* Jaeger, 1833; designated by Deichmann, 1958 : 310).

Halodeima: Cherbonnier, 1964.

DIAGNOSIS: Tentacles 20; pedicels in three distinct but crowded rows on the more or less distinctly 'sole'-like ventral surface, papillae small and irregularly arranged on the dorsal surface; body wall soft, quite thick, usually 2-3 (1-5) mm.; body almost

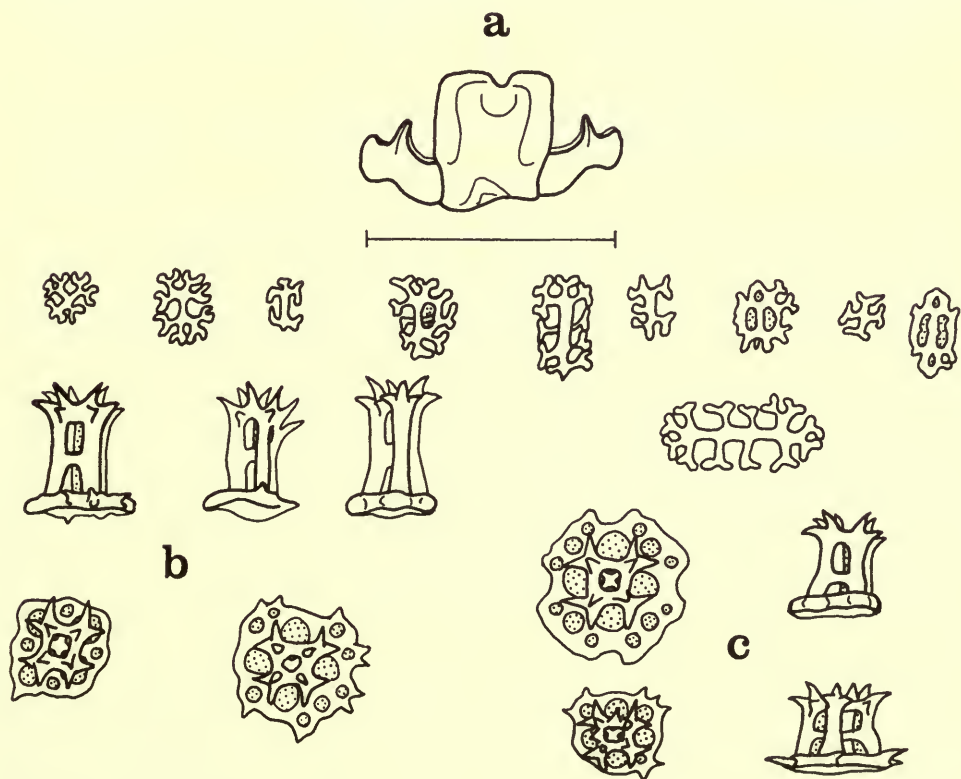


FIG. 7. *Holothuria* (*Halodeima*) *atra* Jaeger, 1833. B.M. No. 1886.10.2.170-171, Amboina, length 120 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0.1 mm. for (b) and (c).

cylindrical; size moderate to large, up to 350 mm. long; calcareous ring quite stout, radial plates up to three times the length of the interradians; spicules consisting of tables usually with reduced disc, spire moderate or high, ending in a few spines forming a maltese cross when viewed from above, *no* large flattened or spinose rods present in the body wall.

OTHER SPECIES INCLUDED: *Holothuria chilensis* Semper, 1868; *H. edulis* Lesson, 1830; *H. floridana* Pourtalés, 1851; *H. grisea* Selenka, 1867; *Stichopus kefersteini* Selenka, 1867; *Holothuria mexicana* Ludwig, 1875; *H. pulla* Selenka, 1867; *Halodeima stocki* Cherbonnier, 1964.

REMARKS: The species of the subgenus *Halodeima* are most readily distinguished from each other by the degree of complexity of the rosettes. These range from simple dichotomously-branched rods, as found in *H. (H.) floridana* from the West Indies, to small perforated oval or round plates (rosettes), as found in the Indo-West Pacific ranging *H. (H.) atra* and another West Indian species *H. (H.) mexicana*. The rosettes are formed by the anastomosis of the dichotomously-branched ends of the rods. The tables are not very variable; those of *H. (H.) mexicana* tend to develop a much more complete disc than usual with a peripheral ring of holes.

Subgenus *ACANTHOTRAPEZA*¹ subgen. nov.

(Text-fig. 8)

(TYPE-SPECIES: *Holothuria pyxis* Selenka, 1867; here designated.)

Holothuria (part): Selenka, 1867; Semper, 1868; Ludwig, 1875.

DIAGNOSIS: Tentacles 20; pedicels irregularly arranged on the ventral side, papillae small to large and conical, arranged irregularly on the dorsal side; body wall soft, fairly thick, usually 3 (2–5) mm.; body almost cylindrical but ventrally sometimes flattened and 'sole'-like; size small to large, up to 350 mm. long; calcareous ring stout, radial plates squarish, up to twice as long as the interradians; spicules consisting of tables in combination with rosettes, tables usually large and clumsy with well-developed spinose disc and low to high spire, the rim of the disc is often turned up to give the tables a cup and saucer appearance in lateral view, in small specimens (? juveniles) the tables with a high spire and smooth-rimmed disc.

OTHER SPECIES INCLUDED: *Holothuria coluber* Semper, 1868; *H. kubaryi* Ludwig, 1875.

REMARKS: The tables of *Acanthotrapeza* resemble those found in *Lessonothuria* Deichmann, 1958. However the presence of rosettes instead of irregular pseudo-buttons separates the two subgenera immediately. The form of the tables separates *Acanthotrapeza* from *Halodeima*, the only other subgenus of *Holothuria* with the combination of tables and rosettes.

The three species are quite easily distinguished from each other. *H. (A.) kubaryi*

¹ Greek: *Acanthodes* = thorny; *trapeza* = a table.

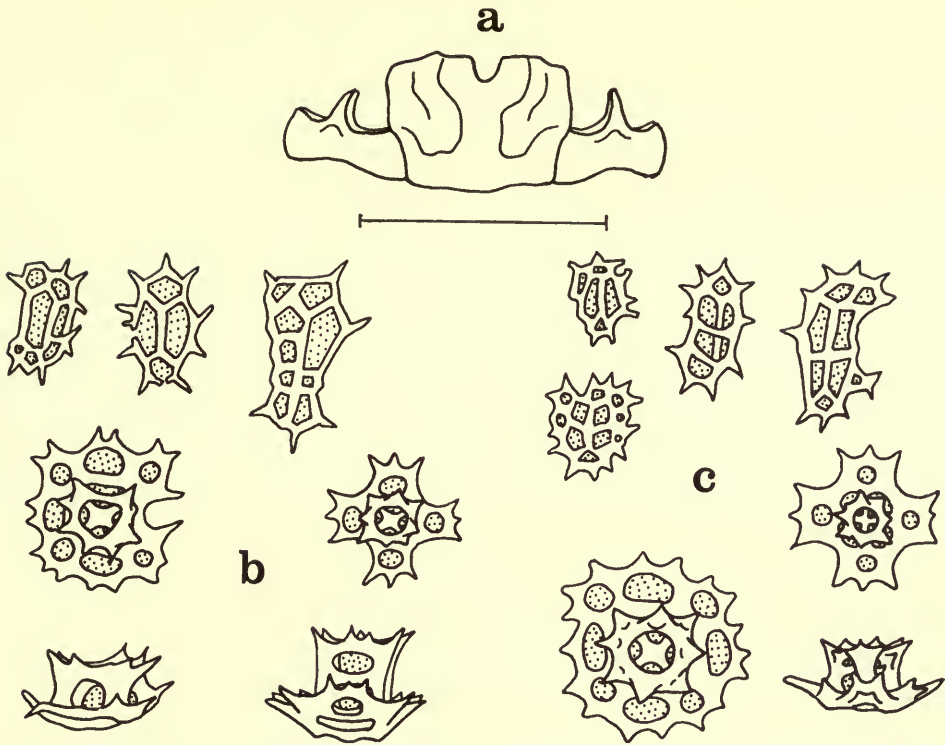


FIG. 8. *Holothuria (Acanthotrapeza) pyxis* Selenka, 1867. B.M. No. 1886.6.26.89-90, syntype of *Holothuria papillata* Bell, 1887, Andaman Islands, length 320 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0.1 mm. for (b) and (c).

from the South Pacific Islands (Samoa and the Solomons) appears to be the smallest (up to 70 mm. according to Ludwig, 1875 and there is a specimen collected from the Solomon Islands in the British Museum of 30 mm. length). The spicules are smooth-rimmed tables with tall spires and relatively simple rosettes. *H. (A.) coluber* from the East Indies, Philippines and northern Australia has very clumsy tables with spinose rim and low to moderate spire; the rosettes are relatively large and complex. *H. (A.) pyxis*, the type-species, from the East Indies and Andaman Islands, is the largest, attaining a length of about 350 mm. The tables are usually low-spired and clumsy and the rosettes not so complex as in *H. (A.) coluber*. A further factor establishing the identity of the last two species is the form of the dorsal papillae. Those of *coluber* are more numerous and smaller than the fewer, relatively large, conical papillae of *pyxis*.

It should be pointed out that the presence of tall-spired tables has sometimes been considered to be correlated with immature size. If this is correct, then *H. (A.) kubaryi* may represent the juvenile stage of another species.

Subgenus **STAUROPORA**¹ subgen. nov.

(Text-fig. 9)

(TYPE-SPECIES: *Holothuria discrepans* Semper, 1868; here designated.)*Holothuria* (part): Semper, 1868; Ludwig, 1875, 1888; Lampert, 1889; Fisher, 1907.

DIAGNOSIS: Tentacles 18–30; pedicels in three distinct rows on the flattened ventral surface, papillae small, irregularly arranged dorsally, a 'collar' of papillae sometimes present around the base of the tentacles; body wall soft, not very thick, usually about 1 (1–2) mm.; body with flattened 'sole'-like ventral side, arched dorsally; size small, up to 100 (rarely 125) mm. long; calcareous ring with radial plates up to three times the length of the interradial plates; spicules consisting of tables with low, moderate or high spire, disc squarish to octagonal with a large centrally-placed cruciform hole and one or more smaller holes alternating with each arm of the central cross giving the disc a very characteristic appearance, the rim smooth or spinose, flat or slightly turned up to give a 'cup and saucer' appearance to the table

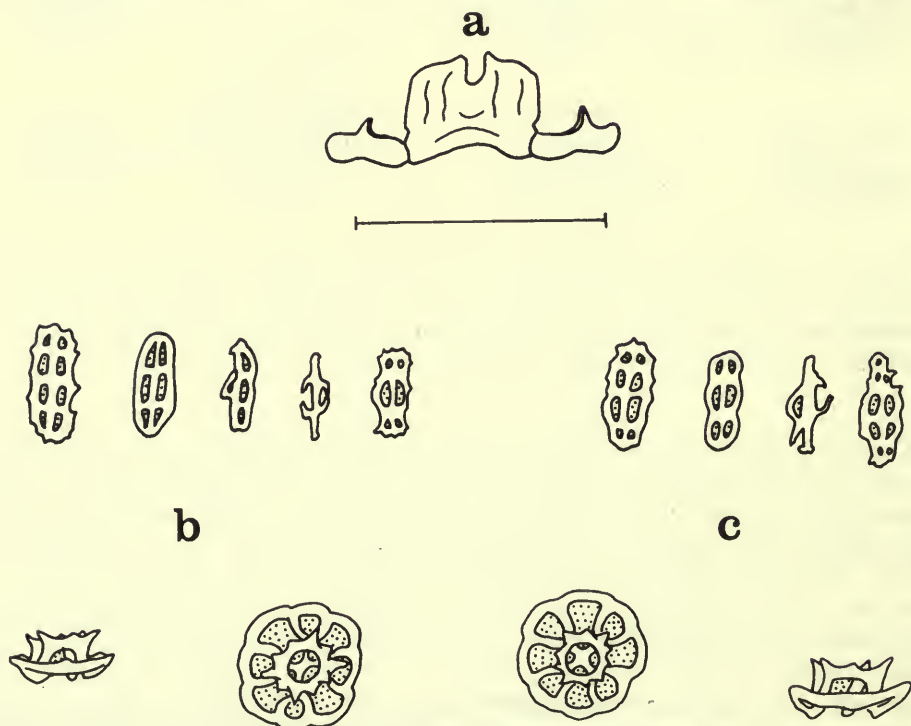


FIG. 9. *Holothuria (Stauropora) discrepans* Semper, 1868. B.M. No. 1874.10.5.23, Samoa (? type material; received from Godeffroy Museum), length 55 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0.1 mm. for (b) and (c).

¹ Greek *Staurus* = a cross; *porus* = a pore.

in lateral view, buttons usually present, rarely totally absent, very variable, oval, smooth or rugose, occasionally incomplete or even reduced to small bars with lateral lobes, complete buttons usually with 3 to 6 pairs of holes.

OTHER SPECIES INCLUDED: *Holothuria annulifera*, *H. fusco-olivacea* and *H. hawaiiensis* Fisher, 1907; *H. ludwigi* Lampert, 1889; *H. modesta* Ludwig, 1875; *H. olivacea* Ludwig, 1888.

REMARKS: The form of the tables in *Stauropora* is a very characteristic feature of this group of species. They are distinguished from each other most readily by the form and occurrence of the buttons. *H. (S.) fusco-olivacea* from Hawaii, northern Australia and the Red Sea, *H. (S.) ludwigi* from Samoa and *H. (S.) olivacea* from the East Indies have small oval rugose buttons reminiscent of those found in the subgenus *Holothuria*. The spicules figured of these three species are so similar that I suspect that they will prove to be synonymous, in which case *H. (S.) olivacea* has priority. *H. (S.) annulifera* from Hawaii has small incomplete knobbed buttons or bars, while the buttons of *H. (S.) discrepans* from the South Pacific Islands and the Maldive Islands and *H. (S.) hawaiiensis* from Hawaii are generally smooth and complete with three to six pairs of holes. The main character separating these last two species can be found in the form of the tables. Those of *H. (S.) hawaiiensis* are of two kinds, tall-spined, flat-disced forms lacking the characteristic cruciform appearance of the central hole, as well as the lower-spined tables characteristic of the subgenus. Only the characteristic tables are found in *H. (S.) discrepans*, the type-species. *H. (S.) modesta* from the East Indies and northern Australia is the only species lacking buttons; its tables have a smooth flat disc with the characteristic arrangement of holes and the spire is usually high and slender (Deichmann has also found scattered rosettes in this species according to H. L. Clark, 1946 : 427).

Subgenus **PANNINGOTHURIA**¹ subgen. nov.

(Text-fig. 10)

(TYPE SPECIES : *Holothuria forskali* Delle Chiaje, 1823; the subgenus is monotypic.)

Holothuria (part): Delle Chiaje, 1823; Koehler, 1927; Mortensen, 1927; Panning, 1929-35.

DIAGNOSIS: Tentacles 20; pedicels in crowded indistinct rows on the flattened ventral surface, papillae conical, irregularly arranged dorsally, a 'collar' of papillae is present around the base of the tentacles; body wall quite thick, usually 2-3 (1-4) mm.; body almost cylindrical but with a flattened ventral 'sole', arched dorsally; size moderate, up to 200 mm. long; calcareous ring quite stout, with radial plates up to twice as long as the interradians, the latter obtusely-pointed anteriorly and with outer surface sometimes slightly concave; spicules consisting of very reduced tables sparsely distributed or even lacking (probably only in badly preserved specimens), having ovoidal disc usually with two to four holes, spire very reduced often present only in the form of 2 or 3 short spines or knobs, buttons totally absent.

¹ Panning + latter part of *Holothuria*, in honour of Dr. A. Panning.

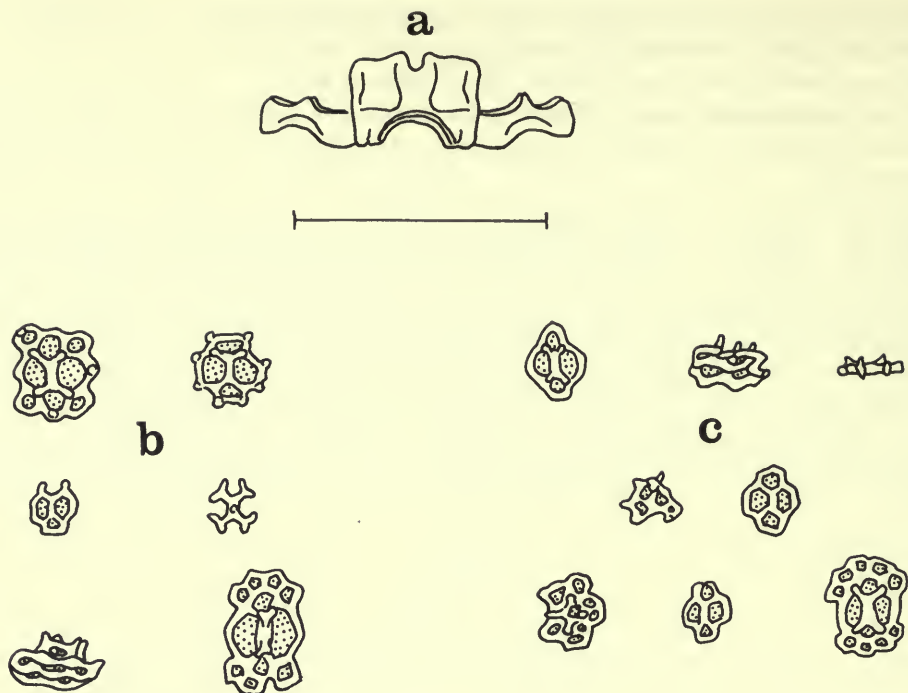


FIG. 10. *Holothuria (Panningothuria) forskali* Delle Chiaje, 1823. B.M. No. 1898.5.3. 292-293, Naples, length 180 mm. (a) Mid-dorsal radial and adjacent interradiar plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0.1 mm. for (b) and (c).

REMARKS: *Panningothuria*, like *Irenothuria*, occupies an isolated position within the genus *Holothuria*. It differs essentially from all the other subgenera in the extreme reduction of its spicules. *H. (P.) forskali* extends from the Mediterranean to the British Isles and Scandinavia.

Subgenus *IRENOTHURIA* Deichmann, 1958

(Text-fig. 11)

Irenothuria Deichmann, 1958 : 306 (Type-species *I. maccullochi* Deichmann, 1958; by monotypy); Caso, 1965.

DIAGNOSIS (after Deichmann but modified to conform with the other diagnoses): Tentacles 20; pedicels arranged in irregular double rows ventrally, papillae similarly arranged dorsally; body cylindrical to bottle-shaped; size small to large, up to 200 mm. long; calcareous ring delicate, low; spicules consisting of a crowded layer of tables, the largest with disc about 0.2 mm. in diameter, with numerous holes and tall spire of four pillars joined by a cross beam near the base, each pillar diverging near the

tip, tapering to a point, also small tables especially in the podia, with shorter spire often reduced to 1-4 knobs or completely lacking.

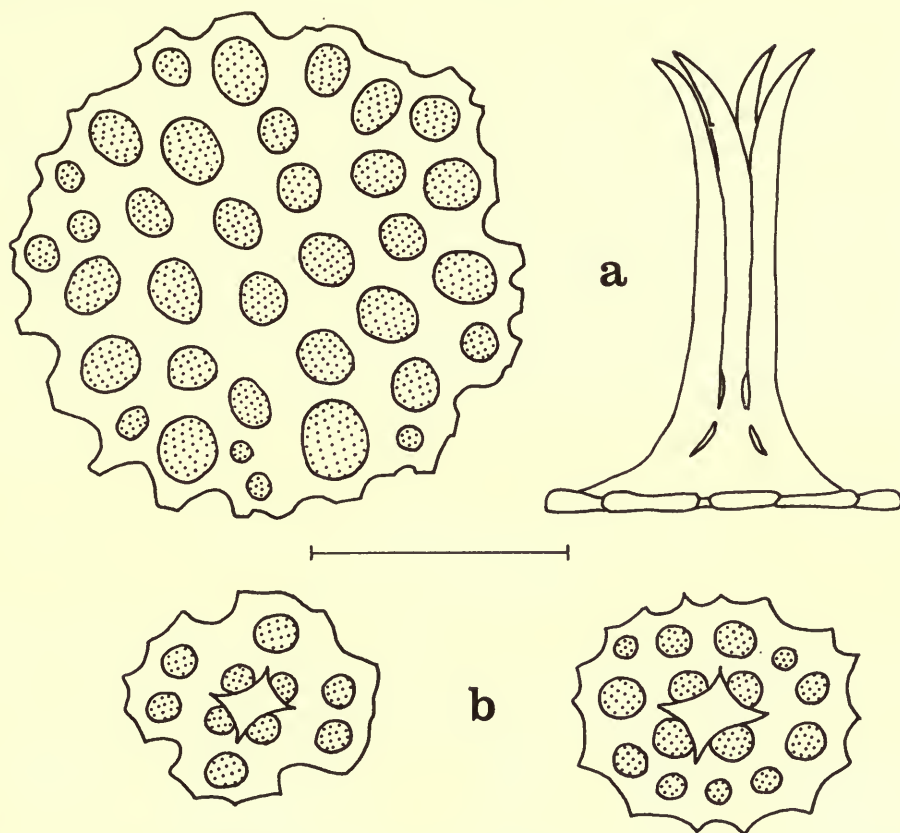


FIG. 11. *Holothuria (Irenothuria) maccullochi* Deichmann, 1958. (a) Disc and profile of large table; (b) small tables seen from above (after Deichmann, 1958, pl. 4, figs. 1-4). The scale measures 0.1 mm.

REMARKS: Deichmann (1958) noted that *Holothuria (Irenothuria) maccullochi*, which ranges from Colombia to the Gulf of California, is 'an unusual form which occupies a position all by itself'. Caso (1965) has recorded the species from Las Galas, west coast of Mexico.

PLATYPERONA¹ subgen. nov.

(Text-fig. 12)

(TYPE-SPECIES: *Holothuria difficilis* Semper, 1868; here designated.)

Muelleria (part): Selenka, 1867.

Holothuria (part): Delle Chiaje, 1823; Semper, 1868.

¹ Greek: *platus* = flat; *perone* = a buckle or button.

Argiodia (part): Pearson, 1914.

H. (Microthele) (part): Panning, 1929.

Microthele: Deichmann, 1958 (non *H. Microthele*) Brandt, 1835. (Type-species *Muelleria nobilis* Selenka, 1867; designated by A. M. Clark & F. W. E. Rowe, 1967a : 100).

DIAGNOSIS: Tentacles 18–20; pedicels crowded, irregularly arranged except in the smaller individuals where they appear to be arranged in three distinct bands on the flattened ventral surface, papillae small, irregularly arranged on the arched dorsal side, a distinct 'collar' of papillae present around the base of the tentacles; body wall soft, not very thick, usually 1–2 (1–5) mm.; body with a distinct flattened ventral 'sole', arched dorsally; size small to moderate, up to 200 mm. long; calcareous ring stout, radial plates about twice as long as the interradiial plates; spicules consisting of well-developed tables, the disc smooth round and flat, with a varying number of peripheral holes, spire of moderate height, ending in several spines, the buttons oval, thin, flat, very rarely with a few median knobs, an apparent median longitudinal ridge is apparent, three to six pairs of relatively small holes.

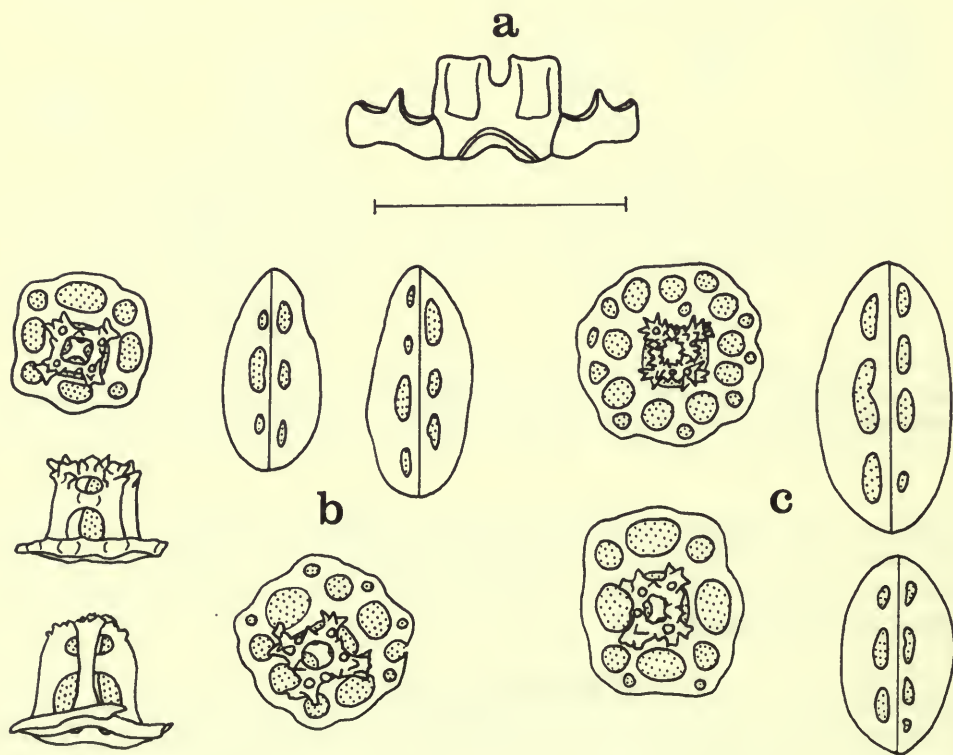


FIG. 12. *Holothuria (Platyperona) difficilis* Semper, 1868. B.M. No. 1898.8.9.21, Rotuma, North of Fiji, length 60 mm. (a) Mid-dorsal radial and adjacent interradiial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0.1 mm. for (b) and (c).

OTHER SPECIES INCLUDED: *Muelleria parvula* Selenka, 1867; *Holothuria sanctori* Delle Chiaje, 1823.

REMARKS: It is unfortunate that neither Panning (1929 and 1939) nor Deichmann (1958) recognized Brandt's (1835) original concept of *H. (Microthele)* since each of them, in the absence of a type-designation by Brandt, inadmissably selected as type-species one not included by Brandt in his subgenus. This is in process of being rectified (see A. M. Clark & F. W. E. Rowe, 1967a), and the new subgeneric name *Platyperona* is now chosen for *H. parvula*, *H. difficilis* and *H. sanctori*.

The distribution of the three species of *Platyperona* is distinctive. *H. (P.) parvula*, the smallest species (up to about 50 mm. long) having relatively narrow, often irregularly-shaped buttons, is distributed throughout the West Indies including Bermuda. *H. (P.) difficilis* which can attain a size of 100–120 mm. length, and has broad, oval, buttons has an Indo-Pacific distribution. *H. (P.) sanctori*, the largest species (up to 200 mm. long), having tables with the disc often possessing an extra-peripheral ring of small holes and buttons which may (rarely) bear a few knobs, is distributed throughout the Mediterranean and eastern Atlantic from Portugal to St. Helena.

Subgenus *THYMIOSYCIA* Pearson, 1914

(Text-fig. 13)

Fistularia (part): Forskaal, 1775.

Holothuria (Fistularia) (part): Lesson, 1830.

Sporadipus (Acolpos) Brandt, 1835 : 35 (Type-species *S. (Acolpos) maculatus* Brandt, 1865; designated by A. M. Clark & F. W. E. Rowe, 1967a, simultaneously proposed for suppression: 98–99, a senior subjective synonym of *Holothuria arenicola* Semper, 1868).

Holothuria (part): Selenka, 1867; Semper, 1868; Lampert, 1885; Theel, 1886; Erwe, 1913; H. L. Clark, 1938.

Stichopus (part): Selenka, 1867.

Holothuria (Thymiosycia) Pearson, 1914 : 171 (Type-species *Fistularia impatiens* Forskaal, 1775; designated by Pearson, 1914 : 164).

Brandtothuria Deichmann, 1958 : 290 (Type-species *Holothuria arenicola* Semper, 1868; designated by Deichmann, 1958 : 290).

Microthele (Paramicrothele) Caso, 1964 : 105 (Type-species *M. (P.) zihuatanensis* Caso; by monotypy).

DIAGNOSIS: Tentacles 18–20; pedicels and papillae usually irregularly arranged ventrally and dorsally, respectively, or occasionally restricted to the ambulacral areas; anal papillae more or less apparent, a 'collar' of papillae usually present around the base of the tentacles; body wall not very thick, usually 2 (1–5) mm.; body rather vermiform; size small to moderate, up to 200 (rarely 250) mm. long; calcareous ring stout, radial plates up to three times the length of the interradiial plates; spicules consisting of fairly stout tables, the flat disc and squarish or irregular in outline, rarely reduced, usually with 8–10 peripheral holes, the spire of moderate height ending in a cluster of small spines, the buttons regular or irregular in outline with three or more pairs of comparatively large holes (except in *H. (T.) arenicola* which has comparatively small holes), not flattened, lacking any appearance of

having median longitudinal ridge, rarely buttons present with slight nodules or forming hollow fenestrated spheres (? *aphanes*).

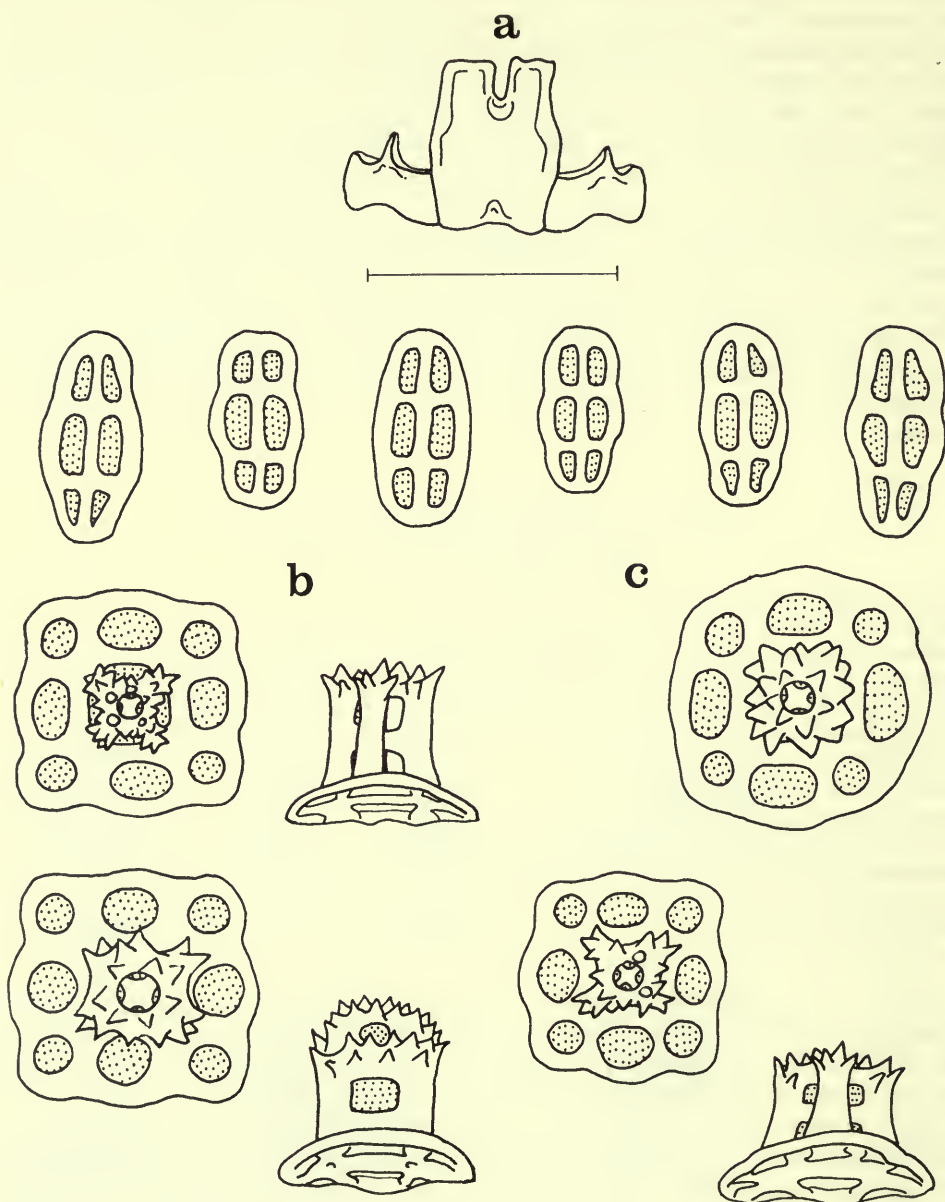


FIG. 13. *Holothuria (Thymiosycia) impatiens* (Forskaal, 1775). B.M. No. 1949.11.7.16, Dahab, Gulf of Aqaba, length 80 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0.1 mm. for (b) and (c).

OTHER SPECIES INCLUDED: *Holothuria aphanes* Lampert, 1885; *H. arenicola* and *gracilis* Semper, 1868; *Stichopus gyriifer* Selenka, 1867; *H. hartmeyeri* Erwe, 1913; *H. (Fistularia) hilla* Lesson, 1830; *H. macroperona* H. L. Clark, 1938; *H. minax* Théel, 1886; *H. remollescens* Lampert, 1888; *H. strigosa* Selenka, 1867; *H. truncata* Lampert, 1885; *Microthele (Paramicrothele) zihuatanensis* Caso, 1964.

REMARKS: Possibly not all the nominal species included above under *Thymiosycia* are valid.

H. (T.) arenicola which is circumtropical is distinguished from the other species by virtue of its small, often reduced, spicules (tables: disc diameter 60 μ ; buttons 50 μ long with comparatively small holes).

H. (T.) remollescens from the Red Sea, Andaman Islands and northern Australia, according to Lampert (1885), has tall-spined tables and smooth six-holed buttons (no measurements can be given here due to lack of material).

H. (T.) aphanes from the Red Sea, Gulf of Aden and East Indies has been considered by Panning (1935) to be conspecific with the circumtropical species *H. (T.) impatiens* Forskaal but since Lampert clearly states that only tables are present in *aphanes*, unlike *impatiens*, I consider it better to reinstate it as a valid species. Cherbonnier (1955) has figured some pseudobuttons from a specimen from the Red Sea which he identified as *H. aphanes* but I do not think that this is correct though lack of relevant material for direct comparison prevents a positive conclusion.

H. (T.) gyriifer from the West Indies, *hartmeyeri* from south west Australia, *hilla* from the Indo-West Pacific area, *macroperona* from northern Australia, *strigosa* from the Red Sea and *zihuatanensis* from South West Mexico, have quite well-developed spicules with tables having the disc round or irregular in outline, usually perforated with > 8 peripheral holes, the spire is moderately high and the buttons have 3–10 pairs of comparatively large holes (tables: disc diameter 65–80 μ ; spire 40–80 μ ; buttons 65–160 μ long).

H. (T.) gracilis from the Philippine and Pelew Islands, the circumtropical species *impatiens*, *minax* from Japan and *truncata* from northern Australia and the East Indies have large robust spicules, the tables have a squarish disc perforated by eight peripheral holes, the buttons have 3–8 pairs of relatively large holes (tables: disc diameter 80–90 μ ; spire 40–75 μ ; buttons 75–105 μ long).

Interspecific distinctions are dependant on the size and other minor differences in the spicules.

Brandtothuria Deichmann 1958, becomes a junior subjective synonym of *Thymiosycia* since its type-species, the circumtropical *H. arenicola* Semper, according to Deichmann is congeneric (by my reckoning consubgeneric) with *Fistularia impatiens* Forskaal, the type-species of *Thymiosycia*.

Similarly I think that Caso's (1964) *Microthele (Paramicrothele)* is a junior subjective synonym of *Thymiosycia* since her description and figures of *M. (P.) zihuatanensis*, the type species by monotypy, show no good reason to suppose that it is not consubgeneric with the *arenicola*, *hilla*, *impatiens*, complex of species. Unfortunately Caso has followed Deichmann's (1958) misuse of the name *Microthele* and has apparently not compared her material with other species from the area among which I suspect *H. (T.) gyriifer* Selenka is very closely allied to *zihuatanensis*. (see appendix.)

Subgenus *MERTENSIOTHURIA* Deichmann, 1958

(Text-fig. 14)

Holothuria (part): Jaeger, 1833; Selenka, 1867; Ludwig, 1898; Koehler & Vaney, 1908; Heding, 1938.*Stichopus* (part): Brandt, 1835.*Mertensiothuria* Deichmann, 1958 : 296 (Type-species *Stichopus leucospilota* Brandt, 1835; designated by Deichmann, 1958 : 297).

DIAGNOSIS: Tentacles 18–20; pedicels crowded or, in smaller (? juvenile) specimens, arranged in three distinct rows ventrally, papillae small, irregularly arranged dorsally, anal papillae or 'collar' of papillae around the base of the tentacles not apparent; body wall variable, soft, ranging from thin to fairly thick usually about 2–3 (1–4) mm.; body almost cylindrical but with a more or less flattened ventral 'sole'; size moderate to large (up to 250 mm. long); calcareous ring stout with radial plates about twice as long as the interradial plates; spicules consisting of not very strongly developed

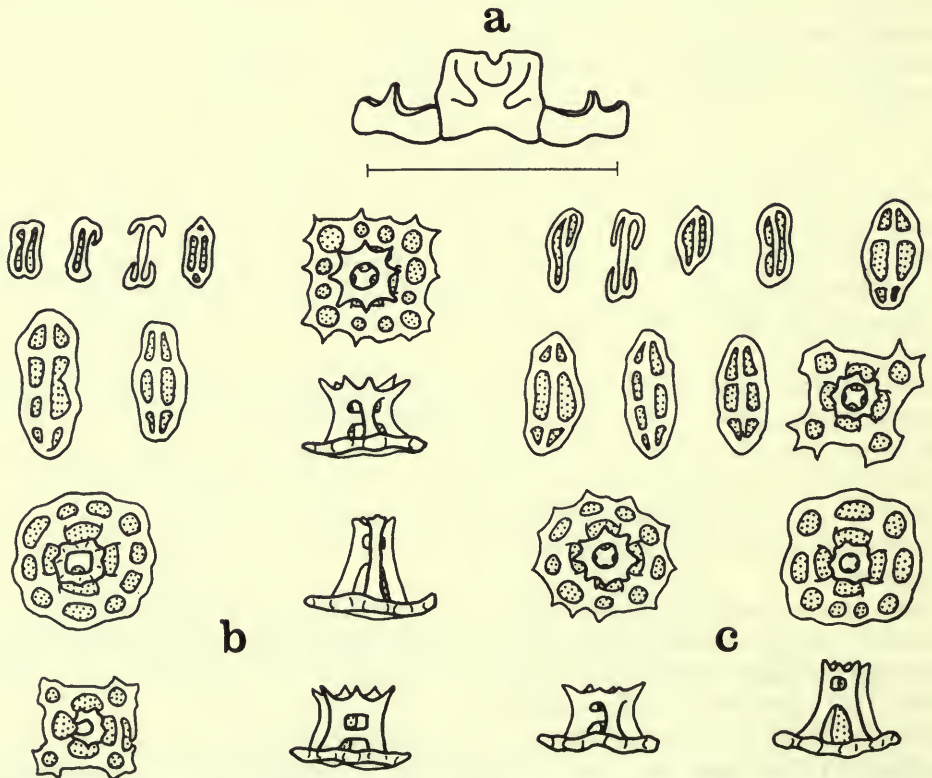


FIG. 14. *Holothuria* (*Mertensiothuria*) *leucospilota* (Brandt, 1835). B.M. No. 1886.10.2. 168, Zamboangan, Philippines, length 80 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0.1 mm. for (b) and (c).

tables with the rim of the disc usually spinose and the spire low, ending in a ring or cluster of spines, the tables occasionally degenerate or incomplete, buttons irregular, usually with three pairs of holes, sometimes incomplete.

OTHER SPECIES INCLUDED: *Holothuria exilis* Koehler & Vaney, 1908; *H. fuscocinerea* Jaeger, 1833; *H. papillifera* Heding, 1938; *H. pervicax* Selenka, 1867; *H. platei* Ludwig, 1898.

REMARKS: The well-known name *Holothuria vagabunda* Selenka, 1867 is a synonym of *leucospilota*, the latter having been placed on the Official List of Specific Names in Zoology (Opinion 762 : 15-18).

Two species, neither of which has been recorded since they were first described, *H. exilis* from the Andaman Islands and *H. papillifera* from the Red Sea are now added to those included by Deichmann in *Mertensiothuria*. Panning (1929-35) merely records *exilis* as a valid species but *papillifera* was described too late for inclusion in his work. I believe, however, that *exilis* will prove to be conspecific with *H. (M.) pervicax* Selenka from the Indo-West Pacific and that *papillifera* may possibly be conspecific with *H. (M.) leucospilota* Brandt also from the Indo-West Pacific.

Deichmann's key (1958) shows the differences between the other species included in this subgenus.

Subgenus **LESSONOTHURIA** Deichmann, 1958

(Text-fig. 15)

Holothuria (part): Delle Chiaje, 1823; Selenka, 1867; Ludwig, 1875; Koehler and Vaney, 1906; Cherbonnier, 1955.

Lessonothuria Deichmann, 1958 : 295 (Type-species: *Holothuria pardalis* Selenka, 1867: designated by Deichmann, 1958 : 295).

DIAGNOSIS: Tentacles 17-30; pedicels and papillae irregularly arranged ventrally and dorsally respectively, a 'collar' of papillae evident around the base of the tentacles, anal papillae usually apparent; body wall soft, not very thick, usually 1 (1-3) mm.; body almost cylindrical but with a more or less distinct, flattened 'sole'; size small to moderate, up to 150 mm. long; calcareous ring fairly stout, radial plates about twice as long as the interradial plates; spicules consisting of clumsy tables, the spire low to moderate and usually terminating in a ring or cluster of spines, disc well developed and spinose, rarely some tables with smooth-rimmed disc also present, rim often turned up to give a 'cup and saucer' appearance to the table in lateral view, pseudobuttons abundant, usually smooth, sometimes spinose, usually irregular in outline and often reduced to a single row of three or four holes, occasionally quite regular buttons are present, with three pairs of holes.

OTHER SPECIES INCLUDED: *Holothuria arguinensis* Koehler & Vaney, 1906; *H. glandifera* Cherbonnier, 1955; *H. insignis* Ludwig, 1875; *H. poli* Delle Chiaje, 1823; *H. verrucosa* Selenka, 1867.

REMARKS: Deichmann (1958) considered *Lessonothuria* to be monotypic, however comparison of the spicules suggests to me that all the above-mentioned species are

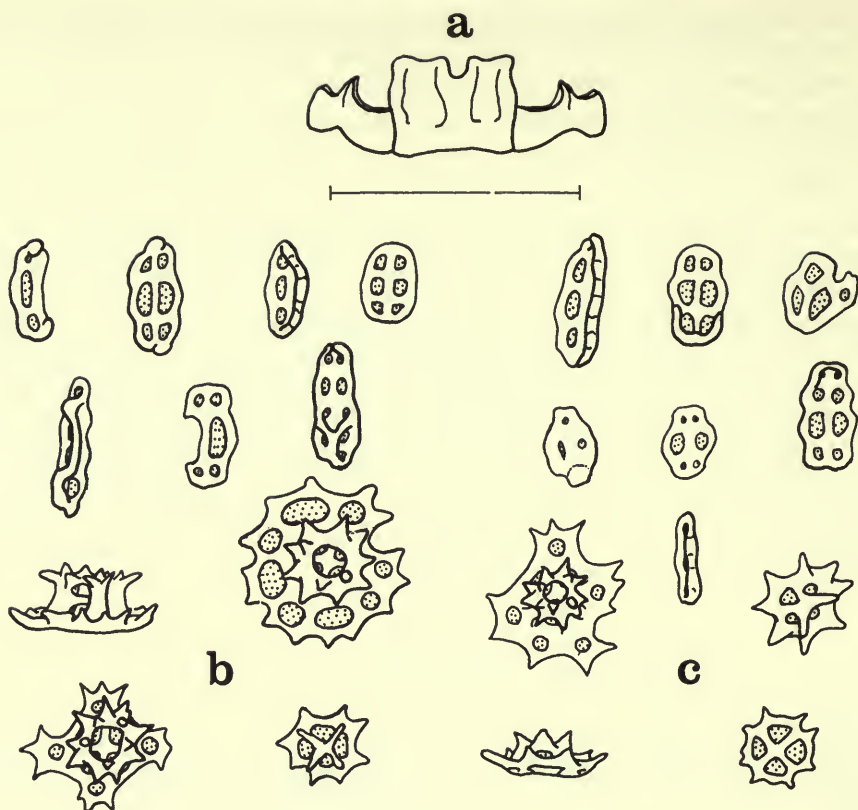


FIG. 15. *Holothuria* (*Lessonothuria*) *pardalis* Selenka, 1867, B.M. No. 1881.10.16.66, Mozambique, length 65 mm. (a) mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0.1 mm. for (b) and (c).

consubgeneric with the Indo-West Pacific type-species *H. pardalis* and should be included here.

H. arguinensis from north-west Africa, the Azores and Canary Islands, *H. poli* from the Mediterranean and *H. verrucosa* another Indo-West Pacific species are well-defined species but I believe that *H. glandifera* from Tahiti and the Persian Gulf and *H. insignis* from the Indo-West Pacific region may prove to be not distinct from *pardalis*.

Panning (1939) considered that *H. arguinensis* belongs in the subgenus *Halodeima*. However, it seems to me more likely that its affinities lie not with *Halodeima atra* (the type-species of *Halodeima*) but rather with *Holothuria pardalis* and *H. poli*.

The form of the tables in this subgenus is very similar to those found in *Acanthotrapeza* but the peculiar form of the pseudobuttons readily separates this group of species from any of the others.

Subgenus *VANEYOTHURIA* Deichmann, 1958

(Text-fig. 16)

Holothuria (part): von Marenzeller, 1893; Koehler & Vaney, 1908; Mortensen, 1925; Deichmann, 1937; Cherbonnier, 1958.

Vaneyothuria Deichmann, 1958 : 307 (Type-species: *Holothuria lentiginosa* von Marenzeller, 1893; designated by Deichmann, 1958 : 308).

DIAGNOSIS: Tentacles 20; pedicels either irregularly arranged or in three bands along the ventral surface, papillae irregularly arranged dorsally though a lateral flange of papillae is sometimes present; body wall soft and muscular, quite thick, about 3 (2-4) mm.; body almost cylindrical but with a flattened ventral 'sole',

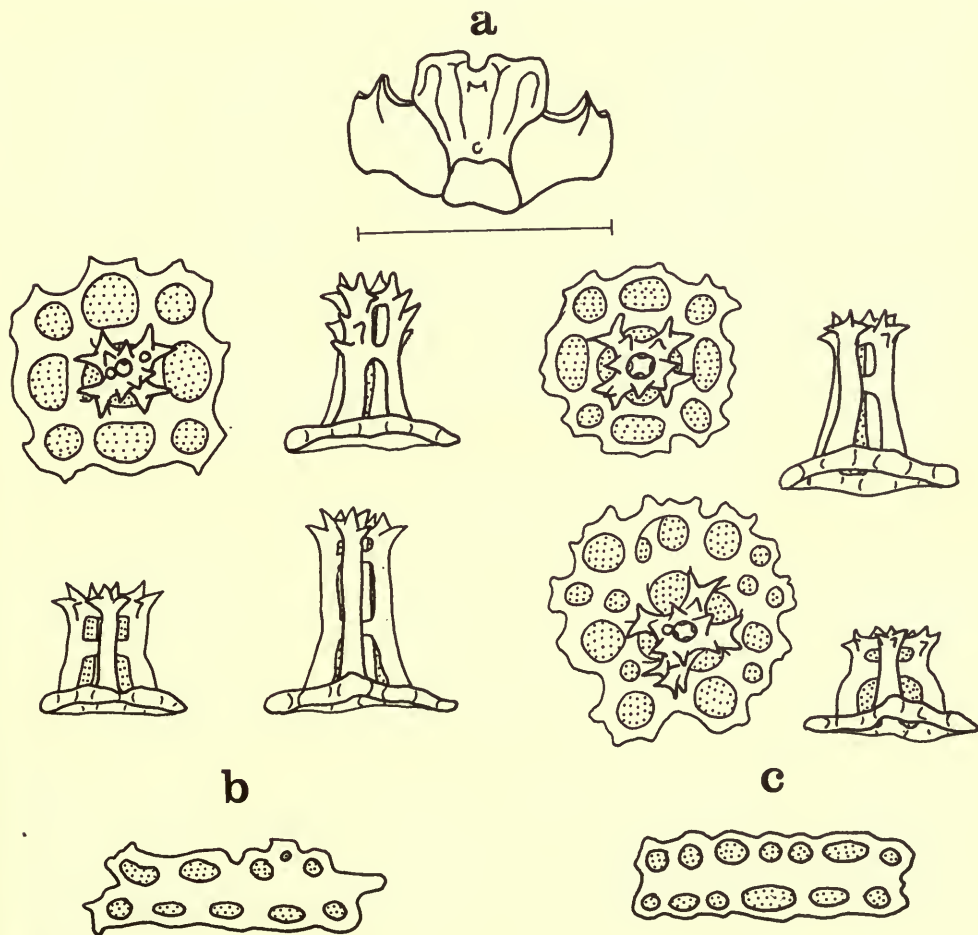


FIG. 16. *Holothuria* (*Vaneyothuria*) *suspecta* Cherbonnier 1958. B.M. No. 1952.4.25.13, Pram Pram, Ghana, length 80 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules of the dorsal and ventral body wall and podia respectively. The scales measure 10 mm. for (a) and 0.1 mm. for (b) and (c).

arched dorsally; size moderate to large, up to 350 mm. long; calcareous ring strongly developed, radial plates about twice as long as the interrarial plates, the latter squarish and obtusely-pointed anteriorly; spicules consisting of well-developed tables, with flat spinose disc, spire of moderate height or high, terminating in several short spines which may give the appearance of a maltese cross when viewed from above, buttons usually scarce, smooth with three to five pairs of holes, often incomplete, irregular or twisted.

OTHER SPECIES INCLUDED: *Holothuria integra* Koehler & Vaney, 1908; *H. neozelanica* Mortensen, 1925; *H. suspecta* Cherbonnier, 1958; *H. zaca* Deichmann, 1937.

REMARKS: Possibly not all of the species included under *Vaneyothuria* are valid since even Deichmann (1958) is doubtful whether *H. neozelanica* from New Zealand is really distinct from *H. integra* from the Bay of Bengal.

Although Cherbonnier (1958) does not affiliate *H. suspecta* from Sierra Leone with any other species it appears to me to be most closely related to *H. lentiginosa*, the type-species of *Vaneyothuria*, and so I include it now in this subgenus. Because of its small recorded size (30 mm.) and the tall-spined tables I strongly suspect that *H. sinefibula* Cherbonnier (1965), also from West Africa, may prove to be synonymous with *suspecta* being merely a juvenile specimen of that species (see remarks for *H. (Acanthotrapeza) kubaryi* p. 139) but until further evidence is available *H. sinefibula* is included here in the list of doubtfully-placed species at the end of this paper.

Deichmann included in *Vaneyothuria* also *Holothuria minax* Théel, 1886; however, after an examination of the type-material I believe *H. minax* from Japan is not consubgeneric with *H. lentiginosa*, from the Azores and Canary Islands, but with the circumtropical *H. impatiens* and accordingly have removed it to the subgenus *Thymiosycia*.

Subgenus **HOLOTHURIA** Linnaeus, 1767

(Text-fig. 17)

Holothuria Linnaeus, 1767 : 1089 (non Linnaeus, 1758, Coelenterata); (Type-species: *H. tremula* Linnaeus, 1767 : 1090 (non Gunnerus, 1767) = *H. tubulosa* Gmelin, 1790 : 3188, validated Opinion 80 1924 : 17-18).

Holothuria (part): Gmelin, 1790; Delle Chiaje, 1823; Grube, 1840; von Marenzeller, 1877; Helfer, 1912; Koehler, 1921 and 1927; Panning, 1939; Cherbonnier, 1954 and 1964. *H. (Thelenota)* Brandt, 1835 : 53 (non H. L. Clark, 1921 : 185, Stichopodidae).

DIAGNOSIS: Tentacles 20; pedicels crowded irregularly on the flattened ventral 'sole', papillae of varied sizes irregularly arranged dorsally, a 'collar' of papillae surrounding the base of the tentacles, anal papillae usually apparent; body wall soft, usually quite thick, about 3 (1-6) mm.; body almost cylindrical but with flattened ventral surface; size small to large, up to 300 mm. long; calcareous ring fairly stout, radial plates about twice as long as the interradians; spicules consisting of simple irregular tables with rather spinose disc which may be somewhat reduced, spire moderate to high, buttons simple, always with numerous small rounded or pointed knobs giving the button a very rugose appearance, three to ten pairs of holes which sometimes become obliterated by the thickening of the button.

OTHER SPECIES INCLUDED: *Holothuria caparti* Cherbonnier, 1965; *H. dakarensis* Panning, 1939; *H. fungosa* Helfer, 1912; *H. helleri* v. Marenzeller, 1877; *H. mammata* Grube, 1840; *H. massaspicula* Cherbonnier, 1954; *H. stellati* Delle Chiaje, 1823.

REMARKS: Deichmann did not take into consideration the predominantly Western Atlantic, Mediterranean, Red Sea group of species of *Holothuria* in her work (1958).

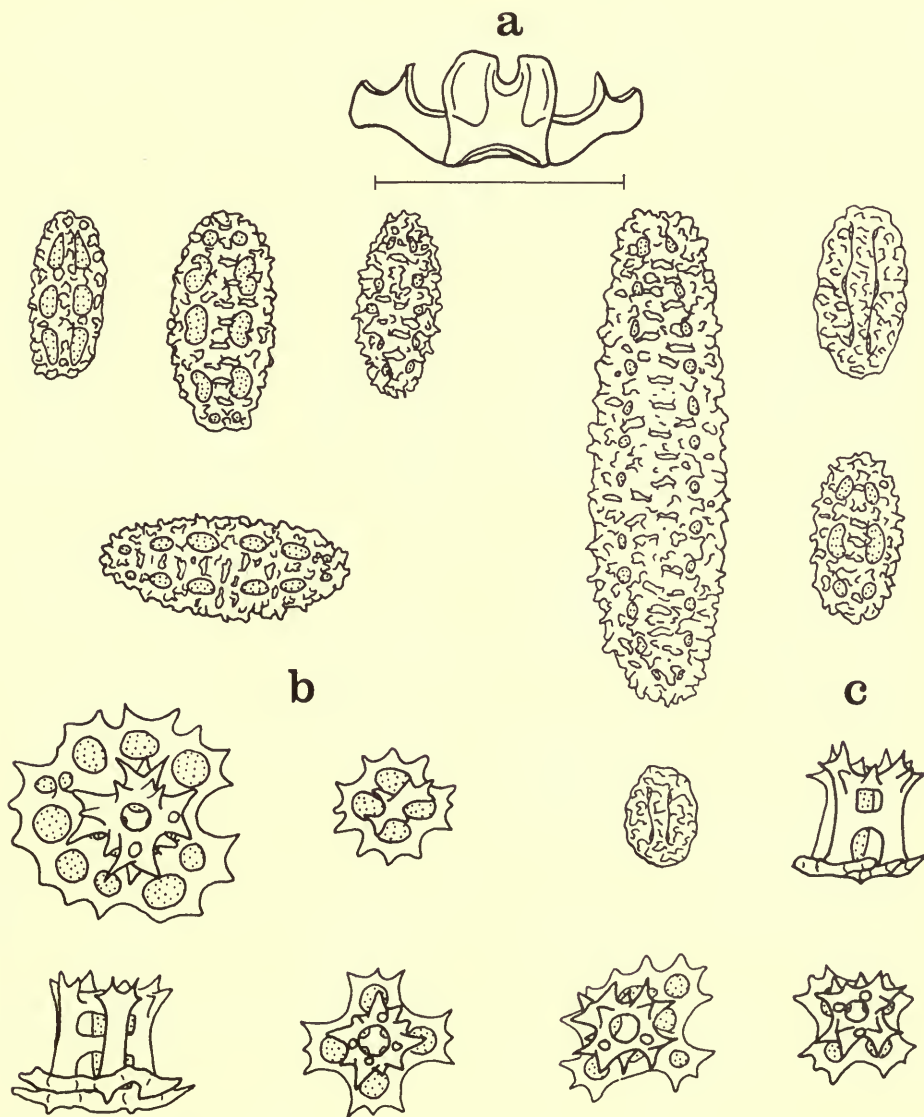


FIG. 17. *Holothuria* (*Holothuria*) *tubulosa* Gmelin, 1790. B.M. No. 1898.5.3.325-326, Naples, length 230 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0.1 mm. for (b) and (c).

Holothuria fungosa and *H. massaspicula*, both from the Red Sea, are clearly con-subgeneric with *H. tubulosa* from the Mediterranean and the Atlantic coasts of France and Portugal and have been treated as valid species by Cherbonnier (1955).

H. caparti from West Africa appears to be most closely related to *H. dakarensis* from the Azores, Canary Islands and West Africa though Cherbonnier (1965) makes no comparison with any other species.

H. helleri from the Mediterranean is a small species, up to 60 mm. long, and correlated with this is peculiar in possessing tables with a very high slender spire and smooth disc. (See remarks for *H. (Acanthotrapeza) kubaryi* p. 139.)

The history of *H. dakarensis*, *H. tubulosa* and *H. mammata* from the Mediterranean and Canary Islands and *H. stellati* from the Mediterranean alone has been somewhat chequered. Koehler (1921 and 1927) considered *tubulosa*, *mammata* and *stellati* to be separate species, giving a good description and figures of each. Panning (1934), however, regarded *stellati* as a variety of *tubulosa*. *H. mammata* he considered still warrants specific rank. In 1939 he treated *stellati*, *tubulosa* and *mammata* as subspecies of *H. stellati* and described a new subspecies, *H. stellati dakarensis*. Cherbonnier (1950) restored *tubulosa* and *mammata* to specific rank, simultaneously elevating *dakarensis* but omitting to consider *stellati*. He considered that *tubulosa*, *mammata* and *dakarensis* can be distinguished not only by their external body form but also by differences in size of the spicules, the smallest being found in *tubulosa* and the largest in *dakarensis*, while *H. mammata* is most easily distinguished from *tubulosa* by its possession of Cuvierian organs. After examining 40 specimens of these species in the British Museum collections I have also found the largest spicules to be present in *H. dakarensis* (tables: disc 65–105 μ diameter, spire 70–85 μ high; buttons 84–160 μ long; Panning's measurements are tables: disc 60–108 μ diameter; spire 60–80 μ ; buttons: 92–172 μ long) but the smallest are in specimens I identify as *H. stellati* (tables: disc 31–52 μ diameter, spire 21–42 μ high; buttons: 31–42 μ , a few up to 75 μ long). The spicules of *H. mammata* and *tubulosa* are intermediate between those of *H. stellati* and *H. dakarensis* (tables: disc 45–85 μ diameter, spire 48–65 μ high; buttons: 40–116 μ long). *H. mammata* can be distinguished from *tubulosa* by its body form with large mammillate dorsal papillae as the name suggests whereas the dorsal papillae of *tubulosa* are smaller, more numerous and cannot be called mammillate. *H. tubulosa* has in general many more elongate, almost solid, buttons (up to about 250 μ long) in the walls of the ventral podia than does *H. mammata*. However use of the presence or absence of Cuvierian organs as a specific character (Cherbonnier, 1950) is unsatisfactory since specimens have often eviscerated before reaching the laboratory.

In the absence of type-material and in order to stabilize the present day concept of *H. tubulosa* I recommend that the description and figures of Koehler, 1921 : 174–176, fig. 130a–g be accepted as a criterion of *H. tubulosa*.

Subgenus *CYSTIPUS* Haacke, 1880

(Text-fig. 18)

Holothuria (part): Selenka, 1867; Ludwig, 1875; Erwe, 1919; Deichmann, 1930; Cherbonnier 1955 and 1964.

Stichopus (part): Selenka, 1867.

Cystipus Haacke, 1880 : 47 (Type-species *C. pleuripus* Haacke, 1880, by monotypy; a synonym of *Stichopus rigidus* Selenka, 1867, according to Deichmann, 1958).

Fossothuria Deichmann, 1958 : 321 (Type-species *Stichopus rigidus* Selenka, 1867; designated by Deichmann, 1958 : 321).

Jaegerothuria Deichmann, 1958 : 322 (Type-species *Holothuria inhabilis* Selenka, 1867; designated by Deichmann, 1958 : 322).

DIAGNOSIS: Tentacles 20; pedicels more or less confined to the ventral ambulacral areas, papillae small and scattered dorsally, a lateral flange of papillae sometimes evident, anal papillae and 'collar' of papillae around the base of the tentacles not



FIG. 18. *Holothuria* (*Cystipus*) *rigida* Selenka, 1867. B.M. No. 1885.7.1.3, Philippines, length 100 mm. (a) Mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 5 mm. for (a) and 0.1 mm. for (b) and (c).

apparent; body wall not very thick, usually about 2 (1–8) mm. often gritty to the touch; body rather vermiform or dorsoventrally flattened; size small to moderate, up to 200 mm. long; calcareous ring fairly stout with radial plates about twice as long as the interradiial plates; spicules consisting of tables with usually knobbed discs and low spire bearing many short spines which are sometimes so numerous and closely crowded that they may almost obscure the disc or become connected to the knobs on the margin of the disc forming a fenestrated sphere (Deichmann, 1958), buttons usually simple with large regularly- or irregularly-arranged knobs, generally 3–4 pairs, but up to 7 pairs, of relatively small holes which may become obscured somewhat by the immensity of the knobs, rarely the buttons modified into fenestrated ellipsoids.

OTHER SPECIES INCLUDED: *Holothuria cubana* Ludwig, 1875; *H. inhabilis* Selenka, 1867; *H. jousseaumei* Cherbonnier, 1955; *H. occidentalis* Ludwig, 1875; *H. pseudofossor* Deichmann, 1930; *H. sucosa* Erwe, 1919; *H. sulcata* Ludwig, 1875; *H. turrisimperfecta* Cherbonnier, 1964.

REMARKS: Possibly not all of the nominal species included above under *Cystipus* are valid.

Deichmann (1958) established two new nominal genera, firstly *Fossothuria* for type-species *Stichopus rigidus* Selenka and including *Holothuria cubana* Ludwig, 1875, secondly *Jaegerothuria* for type-species *H. inhabilis* Selenka, and including *H. occidentalis* Ludwig, 1875. The distinction made between the two appears to rest on regular arrangement of knobs on the buttons in combination with the complexity of the tables in *Fossothuria* as opposed to irregularly-knobbed buttons and relatively simple tables in *Jaegerothuria*. It seems to me that this distinction does not hold good since Deichmann's figures of spicules from the type-material of *rigida* and *inhabilis* show that although the knobs on the longer buttons of *rigida* appear more or less regularly arranged, those on the smaller buttons are just as irregular as those of *inhabilis*. The unmodified tables of the two species are very similar, only those of *inhabilis* do not have as many knobs on the disc. Deichmann further considers that species of *Jaegerothuria* reach a larger size (up to 200 mm. long) than those of *Fossothuria* (60–150 mm. long) though in her description of specimens of *J. inhabilis* she says they range from 70–200 mm. long also that the spicules of the smaller specimens are very similar to *F. rigida*. It seems that smaller individuals of *inhabilis* have more elongate buttons than larger specimens of the same species. It does not appear to me therefore that this character is of subgeneric weight, nor do I feel the difference in the spicules of the respective type-species, *inhabilis* and *rigida*, is sufficiently great to warrant more than a specific distinction. *Jaegerothuria* and *Fossothuria* are therefore treated here as synonyms, *Fossothuria* having priority, but since it shares the same type-species as *Cystipus* Haacke, 1880, namely *Stichopus rigidus* Selenka, 1867, both names fall into synonymy. Although *Cystipus* has not been used since 1880 it is undeniably available (see A. M. Clark & F. W. E. Rowe, 1967a).

In the collections of the British Museum there is a Semper slide marked '*Holothuria rigida* Selenka. Original Zanzibar'. This shows some buttons on which the knobs are more or less regularly arranged whilst other buttons are rather irregular in outline

and knob arrangement. There are a few tables present, these being in the form of fenestrated spheres. Whether these were the only kind of tables present in the specimen it is impossible to say since only a few spicules are present on the slide.

It appears extremely difficult to me to justify the retention of *H. (C.) rigida* from the Indo-Pacific region, *jousseaumei* from the Red Sea and *cubana* from the West Indies as distinct species. Deichmann herself (1958) is inclined to believe that *rigida* and *cubana* are conspecific, separating them only on geographical grounds. Although Cherbonnier (1955) compared *H. jousseaumei* with *H. remollescens* Lampert, 1885, the latter here regarded as consubgeneric with *H. (Thymiosycia) impatiens* Forskaal, judging from Cherbonnier's description and figures, *H. jousseaumei* is most certainly consubgeneric with *H. rigida* and may prove to be conspecific with it. These three nominal species are the only ones which have hollow fenestrated spheres in addition to the knobbed buttons and unmodified tables.

H. (C.) inhabilis from the East Indies, Pacific and Panamic areas is distinguished from *H. (C.) rigida* by its rather simpler tables, lack of fenestrated spheres and rather more irregular buttons.

The West Indian species, *H. (C.) pseudofossor*, like *H. (C.) inhabilis*, is also rather similar to *H. (C.) rigida* but the disc of the tables has only 8 peripheral holes and no hollow fenestrated spheres are present. This species may well prove to be conspecific with *H. (C.) inhabilis*.

H. (C.) sucosa from the Red Sea has tables with 8-10 peripheral holes to the disc and the spire apparently terminating in a ring of irregular spines. The buttons have 4-5 pairs of holes. This species occurs only in the Red Sea and appears to be distinct from all the other species included in *Cystipus*. It seems most closely allied to *H. (C.) rigida* but again differs in lacking the fenestrated spheres.

H. (C.) occidentalis and *sulcata* occur in the West Indian region. *H. (C.) occidentalis* has buttons with 3-5 pairs of holes and simple tables with a knobbed disc and a spire terminating in about four spines. *H. (C.) sulcata* has incomplete or solid buttons and tables with the spire terminating in about twelve spines.

Finally, *H. (C.) turrisimperfecta* from West Africa has buttons with 3-4 pairs of holes, some buttons tending to form ellipsoids, and tables with irregular discs and low spires terminating in 6-8 spines, or the spire may be reduced or lacking. Cherbonnier (1964) compared this species with the West Indian *H. (C.) occidentalis* and *H. imperfector*; the latter according to Deichmann (1958) is conspecific with *H. (Theelothuria) princeps* Selenka, 1867, also from the West Indies.

Subgenus **THEELOTHURIA** Deichmann, 1958

(Text-fig. 19)

Holothuria (part): Selenka, 1867; Semper, 1868; Ludwig, 1875; Lampert, 1885; Theel, 1886; Pearson, 1913; Deichmann, 1937 and 1938.

Theelothuria Deichmann, 1958 : 325 (Type-species *Holothuria princeps* Selenka, 1867; designated by Deichmann, 1958 : 325).

DIAGNOSIS: Tentacles 18-20; pedicels irregularly arranged on the flattened ventral surface, papillae small to large and conical, irregularly arranged dorsally except for the lateral flange of papillae, a 'collar' of papillae usually present around the base

of the tentacles, anal papillae usually apparent; body wall usually very thin and parchment-like, rarely more than 1 (1-2) mm. thick, gritty to the touch; body with a distinctly flattened ventral 'sole', arched dorsally; size moderate to large, up to 250 mm. long; calcareous ring stout and well-developed, radial plates with more or less well developed posterior bifurcations, radial plates up to twice as long as the interradial plates, both radials and interradials may be longer than broad; spicules consisting of well-developed tables with smooth or spinose discs sometimes the disc multi-armed or synallactidlike, spire either low, moderate or high, usually terminating in a cluster of small spines, some tables with perfectly smooth spire tapering to a pointed apex giving the whole table a tack-like appearance usually present also, buttons either simple with irregular moderate-sized knobs or modified into hollow fenestrated ellipsoids.

OTHER SPECIES INCLUDED: *Holothuria hamata* Pearson, 1913; *H. klunzingeri* Lampert, 1885; *H. kurti* Ludwig, 1875; *H. maculosa* Pearson, 1913; *H. notabilis* Ludwig, 1875; *H. paraprinceps* Deichmann, 1937; *H. samoana* Ludwig, 1875; *H. spinifera* Théel, 1886; *H. squamifera* Semper, 1868.

REMARKS: The peculiar features of the calcareous ring in combination with the general form of the spicules sets *Theelothuria* apart from all the other taxa here considered.

H. (T.) maculosa from the western part of the Indian Ocean, *H. (T.) klunzingeri* from the Red Sea and *H. (T.) notabilis* from the East Indies and northern Australia are recognized by the fact that their tables have a low or reduced spire. The degree of reduction of the table is used as the main character to distinguish these species from each other.

H. (T.) samoana from Samoa, *H. (T.) paraprinceps* from the Gulf of California, Panama and westwards to Cocos and the Clarion Islands, *H. (T.) kurti* from the East Indies, Philippines westward to Ceylon and the Red Sea, *H. (T.) spinifera* similarly distributed, *H. (T.) squamifera* from the East Indies, Philippines and east, to the South Pacific Islands and *H. (T.) princeps* from the West Indies, all have well-developed tables.

H. (T.) kurti, *H. (T.) paraprinceps* and *H. (T.) squamifera* are separated mainly on the form of their buttons. Those of *kurti* are elongate with up to 10 pairs of holes while those of *squamifera* have only 3-5 pairs of holes. The synallactid-like tables are not so numerous in *H. (T.) squamifera* as they are in *H. (T.) kurti*. Semper did not mention the presence of synallactid-like tables in his description of *H. (T.) squamifera* but there is a Semper slide of spicules in the collections of the British Museum, presumably from type-material, which shows that such tables are present. *H. (T.) paraprinceps* differs from the other two species in possessing additional tack-like tables and buttons which tend to become smooth with small holes, these holes sometimes becoming obliterated.

H. (T.) princeps and *H. (T.) spinifera* also have some tack-like tables but no synallactid-like tables. They differ from each other in the stouter tables and simpler buttons of *H. (T.) spinifera* while *H. (T.) princeps* has complex ellipsoidal buttons and generally less stout tables.

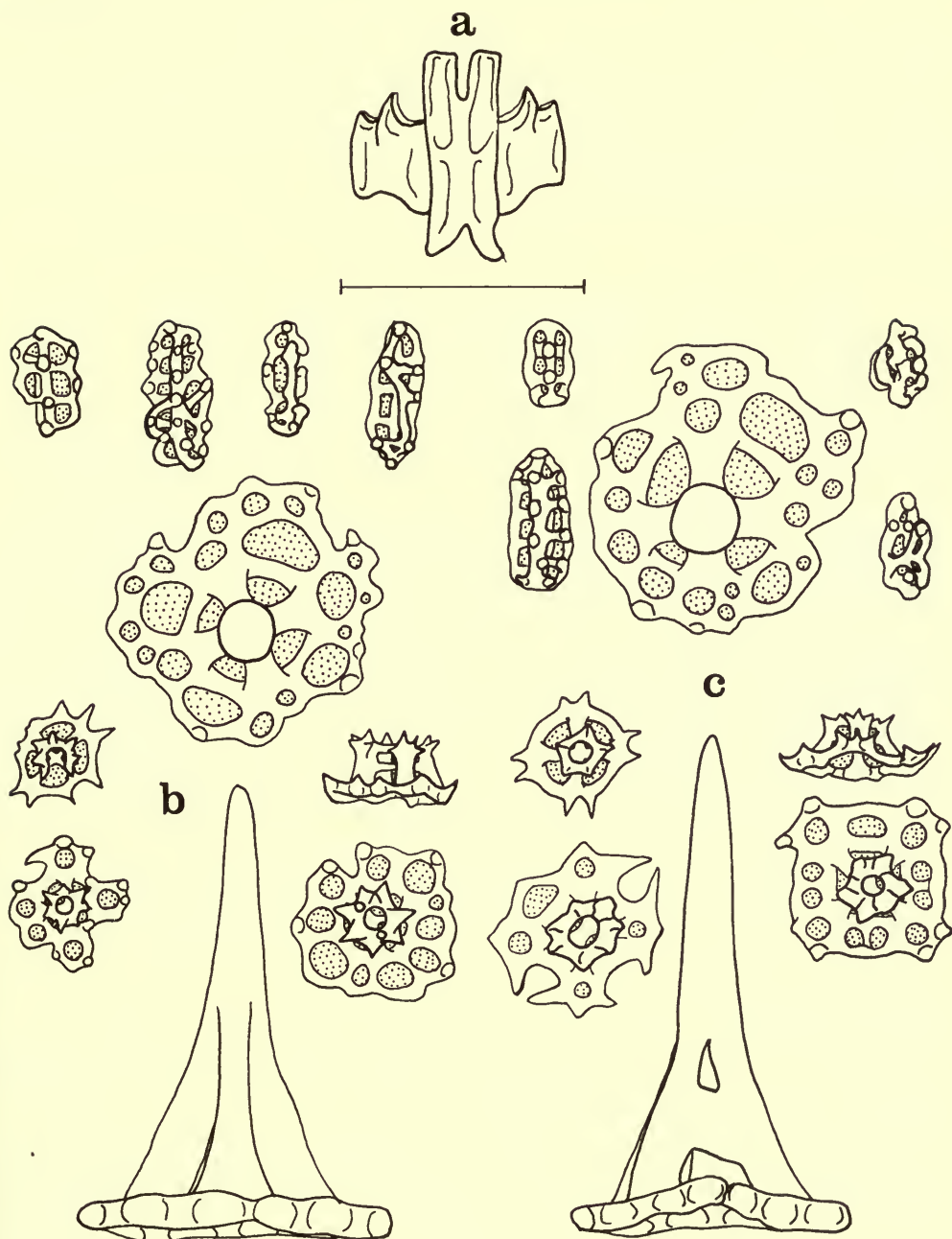


FIG. 19. *Holothuria (Theelothuria) princeps* Selenka, 1867. B.M. No. 1954.9.13.18, Biscayne Bay, Florida, length 120 mm. (a) mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0.1 mm. for (b) and (c).

H. (T.) samoana differs from all the other species in this subgenus by lacking both tack-like and synallactid-like tables. The tables however do have high spires but these terminate in small spines; the buttons have up to 8 pairs of holes.

H. (T.) hamata from the Red Sea is also quite easily distinguished from other species in *Theelothuria*. Tall-spired tables are absent, the tables having spires of moderate height terminating in small spines. The buttons however are usually very irregular and ellipsoidal in form.

METRIATYLA¹ subgen. nov.

(Text-fig. 20)

(Type-species: *Holothuria scabra* Jaeger, 1833; here designated.)

Holothuria (part): Jaeger, 1833; Semper, 1868; Ludwig, 1875; Sluiter, 1901; Helfer, 1912; Erwe, 1913; H. L. Clark, 1938.

DIAGNOSIS: Tentacles 20; pedicels irregularly arranged on the flattened ventral 'sole', papillae usually quite large and conical and irregularly arranged dorsally, a lateral flange of papillae sometimes evident, a 'collar' of papillae around the base of the tentacles often present, anal papillae variously developed; body wall usually quite thin, about 2 (1-5) mm. thick, and gritty to the touch; body usually flattened ventrally, arched dorsally; size small to moderate, up to 200 mm. long; calcareous ring quite well developed with radial plates up to three times as long as the inter-radials; spicules consisting of well-developed tables with smooth disc and spire either of moderate height or high, terminating in a few to many small spines, tables rarely absent, buttons simple, with moderate-sized irregularly arranged knobs and three to ten pairs of relatively large holes.

OTHER SPECIES INCLUDED: *Holothuria aculeata*, *albiventer* Semper, 1868; *H. bowensis* Ludwig, 1875; *H. brauni* Helfer, 1912; *H. martensi* Semper, 1868; *H. michaelsoni* Erwe, 1913; *H. ocellata* Jaeger, 1833; *H. submersa* Sluiter, 1901.

REMARKS: The series of species included in *Metriatyla* were not dealt with by Deichmann (1958).

H. (M.) albiventer from the Indo-West Pacific area is easily distinguished from the other species on account of its solid-looking tables which have spires of moderate height but densely covered with small spines.

H. (M.) aculeata from the East Indies and Philippine Islands and *H. (M.) scabra* from the Indo-West Pacific area have tables with spires of moderate height but they do not terminate in a large mass of small spines. The disc of the tables is perforated by 8-12 holes and the buttons with from 3-5 pairs of holes. Whether these two nominal species are really distinct I seriously doubt. *H. (M.) scabra* has priority.

The tables of *H. (M.) brauni* from the Red Sea are similar to those of *aculeata* and *scabra* but the buttons have from 3-10 pairs of holes.

¹ Greek: *metrius* = moderate; *tylus* = knob.

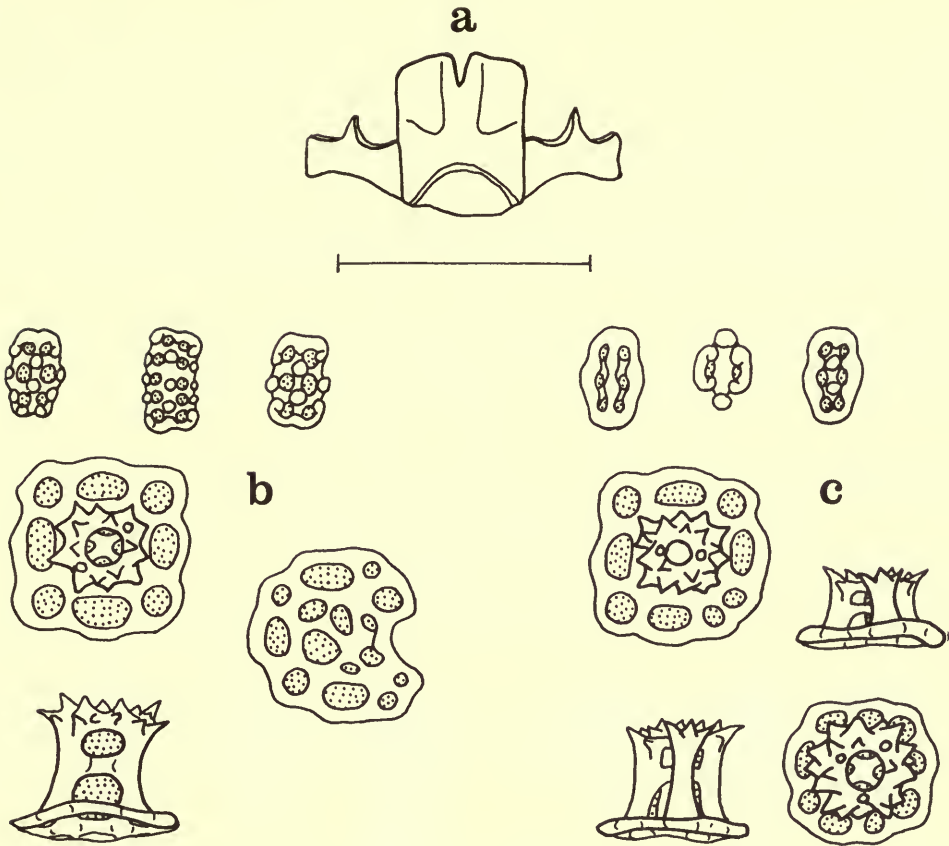


FIG. 20. *Holothuria (Metriatyla) scabra* Jaeger, 1833. B.M. No. 1855.4.4.7, Amboina, length 130 mm. (a) mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0.1 mm. for (b) and (c).

The tables of *H. (M.) ocellata* from the East Indies, Bay of Bengal and Red Sea have spires of moderate height or are slightly higher and the buttons have 3–6 pairs of holes.

The spires of the tables of *H. (M.) bowensis* from northern Australia and *H. (M.) martensi* from the East Indies and Indian Ocean are relatively high, those of *bowensis* having up to five cross-bridges and those of *martensi* up to seven cross-bridges. The buttons of *bowensis* have 3–5 pairs of holes while those of *martensi* usually only have 3 pairs of holes.

H. (M.) michaelsoni from western Australia apparently lacks tables.

H. (M.) submersa from the East Indies has tables which have a spire of four unconnected pillars terminating in numerous small spines. The buttons have 3 to 4 pairs of holes.

Subgenus **MICROTHELE** Brandt, 1835

(Text-fig. 21)

Holothuria (*Microthele*) Brandt, 1835 : 54 (Type-species *H. (M.) maculata* Brandt, 1835 : 54 = *Muelleria nobilis* Selenka, 1867; designated by A. M. Clark & F. W. E. Rowe, 1967a : 100) non *Microthele*: Deichmann, 1958 : 287 = *Platyperona* subgen. nov.).
Holothuria (*Argiodia*) (part) Pearson, 1914 : 170 (Type-species *H. maculata* Brandt; designated by Pearson, 1914) [see A. M. Clark & F. W. E. Rowe, 1967a : 100].

DIAGNOSIS: Tentacles 20; pedicels and papillae indistinguishable, scattered ventrally and dorsally, no apparent 'collar' of papillae around the base of the tentacles,

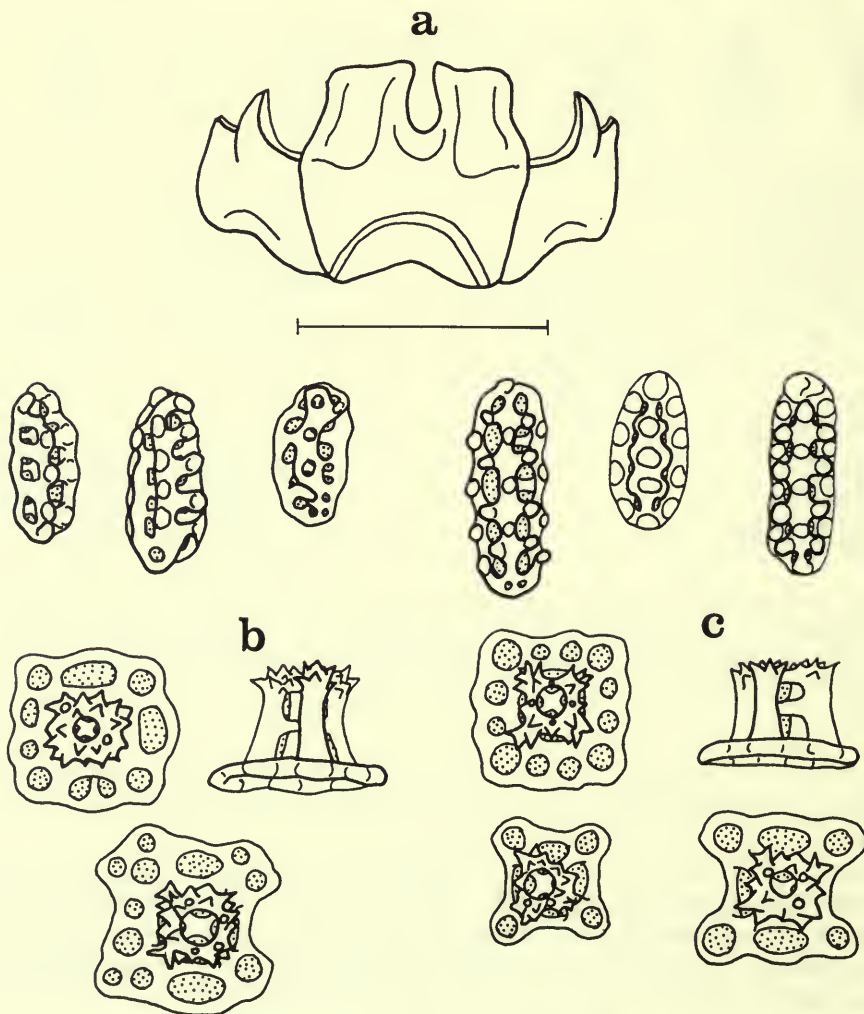


FIG. 21. *Holothuria* (*Microthele*) *nobilis* (Selenka, 1867). B.M. No. 1877.1.15.11, Samoa, length 170 mm. (a) mid-dorsal radial and adjacent interradial plates of the calcareous ring; (b) and (c) spicules from the dorsal and ventral body wall and podia respectively. The scale measures 10 mm. for (a) and 0.1 mm. for (b) and (c).

anus usually with 5 calcified papillae only, though in smaller specimens (up to 200 mm. long) more papillae may be present and in the very large specimens (over 400 mm. long) anal papillae may be entirely lacking; body wall very thick, usually 5 (5-10) mm.; body rather cylindrical; size large or even massive, up to 600 mm. long; calcareous ring massive, with distinctly scalloped anterior margin, radial and interradian plates squarish, the radials being about twice the length of the interradians; spicules consisting of stout, well-developed tables with smooth squarish disc, spire of moderate height terminating in many small spines, buttons usually always hollow fenestrated ellipsoids though a few simple knobbed buttons may be present.

REMARKS: Brandt's concept of *Microthele* is now narrowed to encompass only the single Indo-West Pacific species *Muelleria nobilis* Selenka (see pp. 120 and 145 of this paper; A. M. Clark & F. W. E. Rowe, 1967a : 100). It is isolated by the form of the calcareous ring and spicules in combination with the massive size attained by the animal.

Having examined the holotype of *Holothuria whitmaei* Bell, 1887, in the collections of the British Museum, comparison of the body form, calcareous ring and spicules leads me to conclude that it is conspecific with *H. (M.) nobilis* Selenka.

Caso (1964) has described *Paramicrothele*, a subgenus of *Microthele* sensu Deichmann, non Brandt. The type-species, *M. (P.) zihuatanensis*, I consider is referable to the subgenus *Thymiosycia* (see appendix).

The following table (p. 165), based entirely on spicule occurrence and form may assist in assigning a species to its subgenus, supplementing the evolutionary tree and the key. Entries in brackets indicate the occasional occurrence of that character.

The following list includes synonymies made since Panning's survey of 1929-35. Those made in the present work are marked with an asterisk.

NOMINAL SPECIES LISTED BY PANNING,
1929-35

- Holothuria (Actinopyga) formosa*
(Selenka, 1867).
H. (Microthele) excellens (Ludwig, 1875).
H. (Microthele) flavocastanea (Théel, 1886).
H. (Microthele) bedfordi (Deichmann, 1922).
H. (Microthele) aegyptiana (Helfer, 1912).
H. (Microthele) lubrica (Sluiter, 1894).
Holothuria nitida Ives, 1891.
H. silamensis Ives, 1891.

PRESENT DISPOSITION AND AUTHORITY

- Thelenota ananas* Jaeger, 1833 : Panning, 1944.
H. (Platyperona) difficilis Semper, 1868 :
Deichmann, 1958 (as *Microthele*).
H. (Platyperona) sanctori Delle Chiaje, 1823 :
Deichmann, 1958 (as *Microthele*).
H. (Platyperona) difficilis Semper, 1868 :
Deichmann, 1958 (as *Microthele*).
H. (Cystipus) rigida (Selenka, 1867) :
Deichmann, 1958 (as *Fossothuria*).
? *H. (Mertensiothuria) leucospilota* Brandt, 1835 :
Deichmann, 1958.
H. (Halodeima) floridana Pourtalés, 1851 :
Cherbonnier, 1951.
H. (Halodeima) floridana Pourtalés, 1851 :
Cherbonnier, 1951.

- H. inornata* Semper, 1868.
H. lubrica var. *marenzelleri* Ludwig, 1883.
H. oxurropha Sluiter, 1888.
H. lamperti Ludwig, 1886.
H. immobilis Semper, 1868.
H. frequentiamensis H. L. Clark, 1902.
H. infesta Sluiter, 1901.
H. pertinax Ludwig, 1875.
H. unicolor Selenka, 1867.
H. fuscopunctata Jaeger, 1833.
H. altimensis H. L. Clark, 1921.
H. subverta H. L. Clark, 1921.
H. hypamma H. L. Clark, 1921.
H. fossor Deichmann, 1926.
 * *H. papillata* Bell, 1887.
H. fusco-rubra Théel, 1886.
H. imperator Deichmann, 1938.
 * *H. whitmaei* Bell, 1887.
H. patagonica Perrier, 1904.
H. pluricuriosa Deichmann, 1937.
H. homoea H. L. Clark, 1938.
H. monsuni Heding, 1939.
H. gelatinosa Heding, 1939.
H. pseudo-zacae Cherbonnier, 1951.
H. pseudo-lubrica Cherbonnier, 1951.
H. parinhabilis Cherbonnier, 1951.
H. (Halodeima) kefersteini (Selenka, 1867) :
 Deichmann, 1958 (as *Ludwigiothuria*).
H. (Selenkothuria) erinaceus Semper, 1868 :
 Deichmann, 1958.
H. (Mertensiothuria) leucospilota Brandt, 1835 :
 Deichmann, 1958.
H. (Mertensiothuria) leucospilota Brandt, 1835 :
 Deichmann, 1958.
H. (Lessonothuria) verrucosa Selenka, 1867 :
 H. L. Clark, 1946 (as *Holothuria*).
H. (Platyperona) difficilis Semper, 1868 :
 Deichmann, 1958 (as *Microthele*).
H. (Mertensiothuria) leucospilota Brandt, 1835 :
 Deichmann, 1958.
Labidodemas semperianum Selenka, 1867 :
 Deichmann, 1958.
 ? *H. (Halodeima) grisea* Selenka, 1867 :
 Deichmann, 1930.
 Homonym of *H. fuscopunctata* Quoy & Gaimard,
 1830 : ? syn. of *H. (Cystipus) inhabilis* Selenka,
 1867 : Deichmann, 1958 (as *Jaegerothuria*).
H. (Platyperona) difficilis Semper, 1868 :
 Deichmann, 1958 (as *Microthele*).
H. (Meriatyla) martensi Semper, 1868 :
 H. L. Clark, 1946 (as *Holothuria*).
H. (Cystipus) inhabilis Selenka, 1867 :
 H. L. Clark, 1946 (as *Holothuria*).
H. (Cystipus) cubana Ludwig, 1875 : Deichmann,
 1958 (as *Fossothuria*).
H. (Acanthotrachea) pyxis Selenka, 1867.
H. (Mertensiothuria) leucospilota Brandt, 1835 :
 Deichmann, 1958.
H. (Theelothuria) princeps Selenka, 1867 :
 Deichmann, 1958.
H. (Microthele) nobilis Selenka, 1867.
H. (Thymiosycia) gyrifer Selenka, 1867 :
 Deichmann, 1958 (as *Brandtothuria*).
H. (Mertensiothuria) fuscocinerea Jaeger, 1833 :
 Deichmann, 1958.
H. (Mertensiothuria) leucospilota Brandt 1835 :
 Deichmann, 1958.
H. (Thymiosycia) arenicola Semper, 1868 :
 Deichmann, 1958 (as *Brandtothuria*).
H. (Mertensiothuria) leucospilota Brandt, 1835 :
 Deichmann, 1958.
H. (Mertensiothuria) fusco-cinerea Jaeger, 1833 :
 Deichmann, 1958.
H. (Selenkothuria) lubrica Selenka, 1867 :
 Deichmann, 1958.
H. (Cystipus) inhabilis Selenka, 1867 :
 Deichmann, 1958 (as *Jaegerothuria*).

TABLE I

	TABLES										SPIRE					MODIFICATIONS				BUTTONS					OTHER SPICULES			
	Disc					Terminating in cluster or ring of spines					Terminal spines in maltese+	Low	Medium height	High	Spheres	Synalactid-like	Tack-like	Absent rare or reduced	Smooth	Rugose	Medium sized knobs	Large knobs	Ellipsoidal	Reduced	Absent or rare	Pseudo-buttons	Rods +/or plates	Rosettes
Selenothuria						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Semperothuria						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Halodeima						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Acanthotrachea						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Lessonothuria						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Vaneyothuria						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Thymiosycia						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Platyperona						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Metriatyla						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cystipus						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Microthele						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Theelothuria						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Mertensiothuria						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Stauropora						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Holothuria						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Irenothuria						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pannigothuria						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

Inevitably with such a large assemblage of nominal species there is a residue of some which are currently recognized as probably valid but which it has been impossible to refer to a subgenus, either due to lack of material or to inadequacy of the original description. These are listed here.

NOMINAL SPECIES	POSSIBLE DISPOSITION
<i>Holothuria axiologa</i> H. L. Clark, 1921.	? <i>H. (Microthele)</i>
<i>H. conica</i> H. L. Clark, 1938.	? <i>H. (Metriatyla)</i>
<i>H. cumulus</i> H. L. Clark, 1921.	? <i>H. (Lessonothuria)</i>
<i>H. dietrichi</i> Ludwig, 1875.	? <i>H. (Mertensiothuria)</i>
<i>H. enalia</i> Lampert, 1885.	? <i>H. (Halodeima)</i>
<i>H. isuga</i> Mitsukuri, 1912.	? <i>H. (Lessonothuria)</i>
<i>H. marginata</i> Sluiter, 1901.	? <i>H. (Thymiosycia)</i>
<i>H. sinefibula</i> Cherbonnier, 1965.	? <i>H. (Vaneyothuria)</i>
<i>H. prompta</i> Koehler & Vaney, 1908.	? <i>H. (Stauropora)</i>
<i>H. sluiteri</i> Ludwig, 1888.	? <i>H. (Stauropora)</i>
<i>H. mitis</i> Sluiter, 1901.	?

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APPENDIX

Since the completion of this paper, thanks to the kindness of Dr. Caso, I have received a paratype of *Holothuria (Paraholothuria) riojai* Caso and one of *Microthele (Paramicrothele) zihuatanensis* Caso. These yield the following conclusions:

a. *M. (Paramicrothele) zihuatanensis* in my opinion is close to, if not conspecific with *H. (Thymiosycia) gyrifer* Selenka, 1867, the relationship of which with *hilla* Lesson, 1830, remains to be decided. *Paramicrothele* is therefore referable to the synonymy of *H. (Thymiosycia)*. This agrees with my provisional conclusion expressed on p. 147.

b. *H. (Paraholothuria) riojai* may be a valid species. It is affiliated to the subgenus *Halodeima*, differing only in the absence of rosettes and extreme reduction of the tables. However, in the specimen sent, the spicules appear somewhat eroded by poor preservative. Also there is no sign of the plate-like spicules (resembling those of the sympatric *Pseudocnus californicus*—a dendrochirotid—but unlike anything found in other aspidochirotid) described by Dr. Caso as occurring in this species.

In my opinion *Paraholothuria* could be recognized as a subgenus of *Holothuria* distinguished from *H. (Halodeima)* by the lack of rosettes, though further study may not substantiate this.

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FRONTAL CALCIFICATION AND ITS
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OTHER CHEILOSTOME BRYOZOA



G. P. LARWOOD

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By GILBERT POWELL LARWOOD

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INTRODUCTION

In the course of a general systematic revision certain basic patterns become evident in the structure of the frontal walls of cribrimorph bryozoans. From membranimorph precursors the cribrimorphs evolved increasingly complex structures in the elaboration of both secondary and tertiary frontal walls. These changes may be traced from a phase of diversification in the Cenomanian into the late Cretaceous and Caenozoic. The structure of Recent cribrimorph frontal walls tends to resemble that of the less heavily calcified Cretaceous forms. The extensive tertiary frontal wall calcification of some later Cretaceous cribrimorphs may be interpreted as a feature relating to the whole zoarium. Less marked frontal calcification in some Recent non-cribrimorph cheilostome bryozoans may be similarly interpreted.

THE SECONDARY FRONTAL WALL

EARLY Upper Cretaceous cheilostome bryozoans include genera with marginal spines which arched over the chitinous frontal membrane (the primary frontal wall) but which were not fused along the mid-line of the zooecia (Text-fig. 1*b*). *Anaptopora* and *Anotopora* from the Cenomanian are examples of such genera (Lang, 1961; 1921). Morphologically such genera demonstrate the derivation of cribrimorph costate secondary frontal walls from a membraniporid condition (Text-fig. 1*a*) (Lang, 1921; Larwood, 1962). In the Cenomanian such genera as *Otopora* and *Calpidopora* show the early development of costae firmly fused in the mid-line of the zooecia (Text-fig. 1*c*). In *Otopora* the costae are continuous with no intercostal spaces (Text-fig. 1*e*) and the same structure may be developed in *Hybopora* and *Kankapora* and in the uniserial genus *Corymboporella*, but these Cenomanian genera are imperfectly known. *Calpidopora* represents the more general condition with prominent and undivided intercostal spaces (lacunae).

The frontal structure of *Ctenopora*, another Cenomanian genus, in which subjacent calcareous tissue fills the intercostal spaces, is not found in other Cretaceous cribrimorphs (Text-fig. 1*d*). The Recent bicellariellid genus *Petalostegus* (Text-fig. 2) may

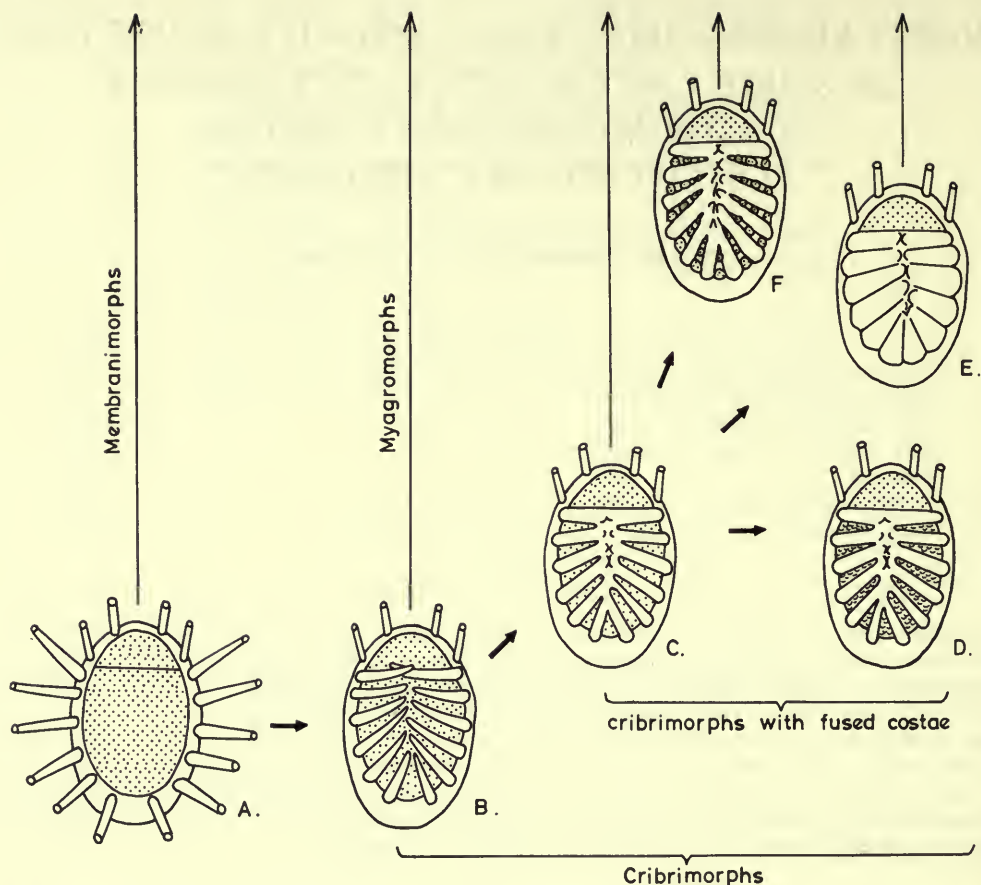


FIG. 1. Diagrams of single zoecia of a membranimorph and of derived early Cretaceous cribrimorphs to show variations in the structure of costate secondary frontal walls.

be cited as achieving a comparable secondary frontal wall of five flat plate-like spines with thickened edges and intervening pores. The porous thickened edges resemble irregular costae with pelmata (lumen pores) but their origin is clearly different from the costae connected by a subjacent lamina in *Ctenopora*.

Some Cenomanian cribrimorphs have divided intercostal spaces (Text-fig. 1f). *Polyceratopora euglypha* shows this condition but the precise nature of the lateral costal fusions is not clear. The Recent genus *Membraniporella* is most closely comparable to early Cretaceous cribrimorph genera of simple structure in which a few irregular lateral costal fusions are developed. *Membraniporella nitida* (Text-fig. 3) has these features but *M. marcusii* (Text-fig. 4) and *M. aragoi* (Text-fig. 5) demonstrate the formation of a costate secondary frontal wall from marginal spines which branch distally in one plane. In Cretaceous cribrimorphs the secondary frontal wall appears always to be formed by unbranched spines.

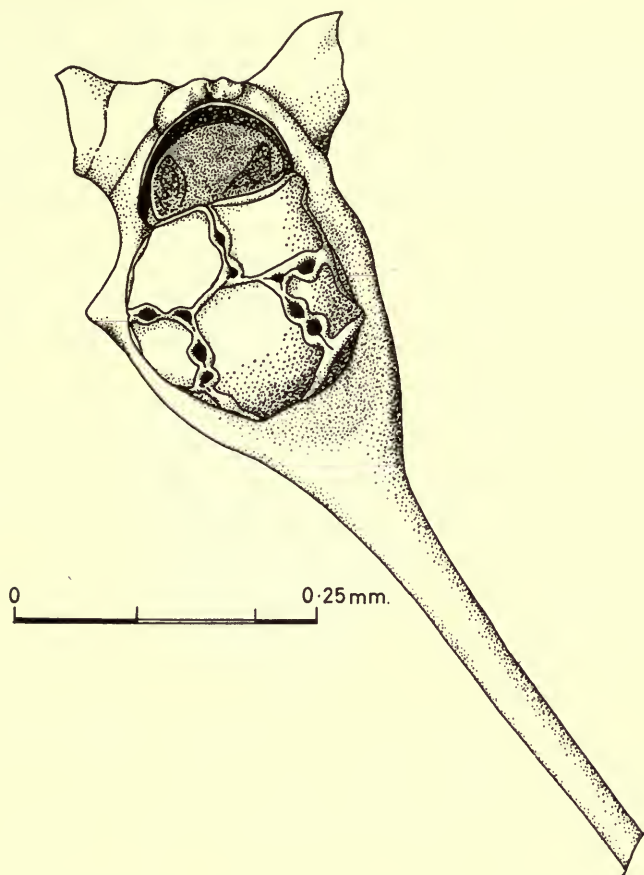


FIG. 2. *Petalostegus bicornis*. Recent. Single zoecium and paired distal-lateral avicularia. B.M.(N.H.) Zool. Dept. 99.7.1.3657.

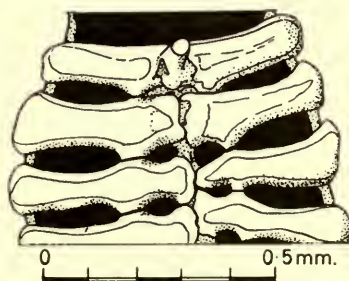


FIG. 3. *Membraniporella nitida* var. *intermedia*. Recent. Distal part of the costate secondary frontal wall of an adult zoecium. B.M.(N.H.) Zool. Dept. 08.3.23.2.

Only *Stichocados* among the Cretaceous genera assigned by Lang (1916, 1921) to the Cribrimorpha possesses minute branched spines on the secondary frontal wall. Current research by Mr. Håkansson, on extremely well preserved specimens of *Stichocados verruculosus* Marsson (1887) from the Danish Maastrichtian White Chalk, indicates that the secondary frontal wall in this genus lacks the hollow tapered costae characteristic of Cretaceous cribrimorphs. The secondary frontal wall is an expansion of calcareous tissue with rather regularly developed openings. Additional minute branched spines occur sparsely on the distal parts of the frontal wall and are most commonly developed adjacent to larger disto-lateral openings. The spines stand up at right angles to the surface of the frontal wall. I am not aware of similar structures occurring in true Cretaceous cribrimorphs and *Stichocados* should perhaps be referred to the Exechonellidae Harmer (1957 : 651) since the genus seems to have affinity with *Exechonella* Canu & Bassler (1927).

Another genus which possesses small branched spines on the secondary frontal wall is *Teuchopora* Neviani (1895). Harmer (1957, p. 896) has discussed this genus and Osburn (1940, p. 411) described a new species, *Teuchopora* (*Coleopora*) *americana*, which he placed in the Petraliidae. The species possesses thin, straight, distally branched spines on the secondary frontal wall (cf., B.M.(N.H.) Zool. Dept. specimen 1965.8.2.7). This example is most comparable with *Stichocados*.

Among post-Cenomanian Cretaceous cribrimorphs different species of *Pelmatopora* demonstrate the principal complications of the costate secondary frontal wall. Earlier species of *Pelmatopora* have undivided intercostal spaces (e.g., *P. solearis*, *P. d'orbigny*). Such species as *P. fecampensis* and *P. pero* possess lateral costal fusions near the mid-line of the zooecium. *P. simplex*, *P. brydonei* and *P. gregoryi* are examples of species with costae joined by many lateral costal fusions. Larwood (1962) illustrates these species of *Pelmatopora*.

An additional, though by no means invariably developed, feature of cribrimorph costae is the presence of pores on the upper surface. These lumen pores are visible in some Recent cribrimorphs as small uncalcified areas which are occupied in life by soft tissue. Similar pores in the costae of fossil cribrimorphs may be termed pelmata and pelmatidia (large and small pores respectively). All species of *Pelmatopora* display pelmata or pelmatidia in the upper walls of the costae. In species with no lateral costal fusions a single pelma is commonly situated near the distal (inner) end of each costa. In species with a well developed series of lateral costal fusions a graded series of pelmata and pelmatidia occurs with the pelmata opposite each lateral costal fusion. In both fossil and Recent cribrimorphs pelmata and pelmatidia may be absent as in *Membraniporella nitidia* and *Cribrilaria radiata*. In some fossil genera pelmata and pelmatidia occur in some species of a genus but not in others. Compare, for example, *Leptocheilopora tenuilabrosa* with *L. vulnerata* (Larwood, 1962).

Among later Cretaceous cribrimorphs *Castanopora jurassica* exemplifies a marked development of pelmata, pelmatidia and lateral costal fusions (Larwood, 1962), and species of *Ubaghsia* such as *U. reticulata* and *U. ornata* demonstrate features developed by some heavily calcified forms in which there are very few pelmata on each costa and a small number of robust lateral costal fusions.

Although there are minor variations the basic pattern of this type of secondary

frontal wall is the same in Cretaceous and in many Recent cribrimorphs. The Recent species *Figularia figularis* has a single pelma at the proximal (outer) end of each costa and *Cribrilina punctata* has a series of nearly equal pelmatidia on each costa.

The structure of the costae in some other Recent cribrimorphs appears to be different. In *Gephyrotes nitido-punctata* prominent pelmata-like structures lie on the intercostal radii and the situation appears to be the same in *Puellina gattyae*. However, in both species small pores occur also above the median lumen of each costa and

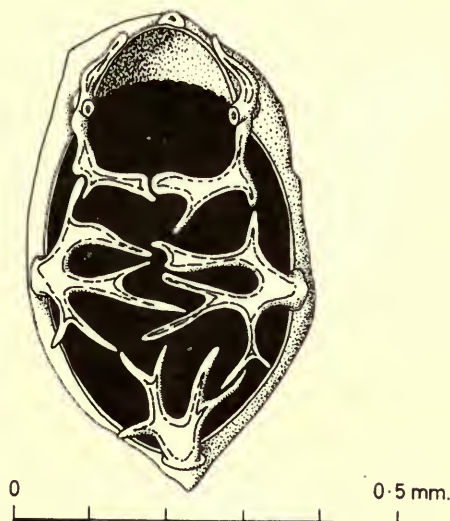


FIG. 4. *Membraniporella marcusii*. Recent. Single adult zooecium.
B.M.(N.H.) Zool. Dept. LIX H.

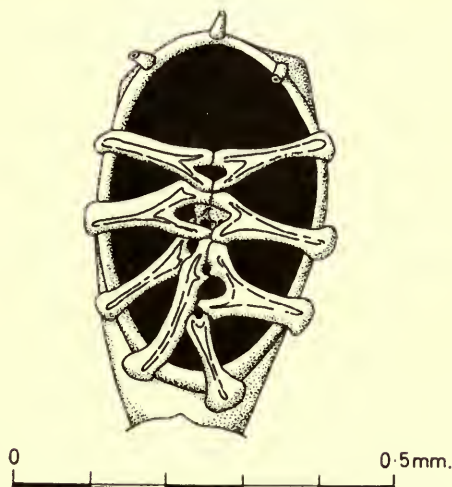


FIG. 5. *Membraniporella aragoi*. Recent. Single adult zooecium.
B.M.(N.H.) Zool. Dept. 1965.8.6.2.

these may be interpreted as normal pelmatidia maintaining the same basic pattern of many other cribrimorphs.

Cribrilaria radiata (Text-fig. 6) has a distinctive and different frontal wall structure not seen in other Recent genera and, with the possible exception of *Corbulipora*, not known fossil. In *Cribrilaria* the costae rise steeply from the margins of the frontal wall forming a peripheral ring of near-vertical hollow spines. At the level of the secondary frontal wall each of these spines branches inward to form costae which lack pelmata or pelmatidia. McGillivray (1895) first described *Corbulipora* from the Middle Miocene of Victoria, Australia. The frontal wall of *Corbulipora* was described as being "... raised, formed by a series of vertical ribs on each side, turning abruptly inwards and uniting to form a flat plate; ...". I have not yet been able to examine specimens of this genus. McGillivray (1895) recognized three species (*C. ornata*, *C. cornuta* and *C. elevata*) and Maplestone (1901) described another species (*C. ampulla*) as having a "... front much raised, with large margined pores, irregularly disposed on the surface; the sides with a regular series of upright elongate pores ...". Brown (1958) described *C. pennata* with a "... frontal shield flattened, consisting of a raised platform of spines projecting outwards laterally ...". I cannot envisage the precise nature of *Corbulipora* in relation to *Cribrilaria*, but it appears that the structure of the secondary frontal wall may be analogous in these genera.

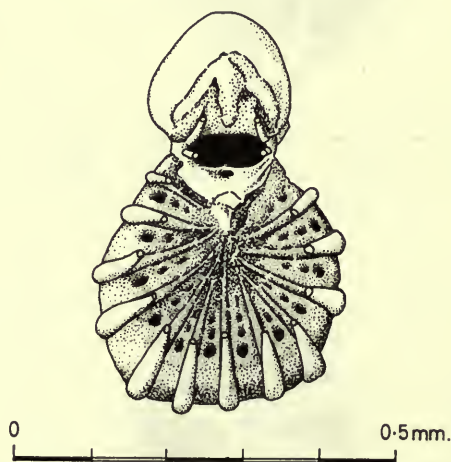


FIG. 6. *Cribrilaria radiata*. Recent. Single adult zooecium with hyperstomial ovicell. B.M.(N.H.) Zool. Dept. 99.5.1.720.

THE TERTIARY FRONTAL WALL

Numerous genera of later Cretaceous cribrimorphs develop a tertiary frontal wall of abundant calcareous tissue above the secondary costate frontal wall. Tertiary frontal walls are well displayed by *Tricephalopora*, *Phractoporella*, *Polycephalopora*, *Coelopora*, *Steginopora*, *Disteginopora* and *Ubaghsia*. In these, and in other genera, there is a general development of calcareous tissue which fills the interzooecial furrows covering the proximal gymnocyst of zooecia and often expanding onto the proximal and lateral

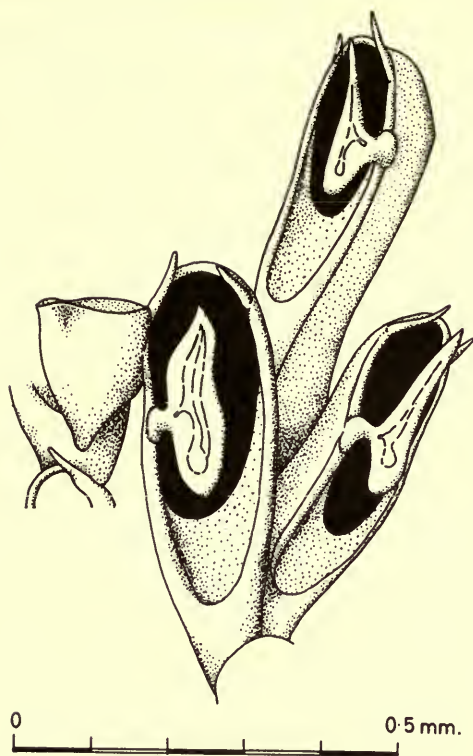


FIG. 7. *Canda clypeata*. Recent. Adult zoecia and an associated avicularium.
B.M.(N.H.) Zool. Dept. 28.9.13.113.

areas of the costate secondary frontal walls. There is general upgrowth of the circum-oral tissue commonly incorporating avicularia and proximal and distal oral shields which result from the enlargement and fusion of distal and lateral oral spines with the enlarged apertural bars. In such genera as *Ubaghsia* this extra calcification forms an irregular robust and raised lattice of calcareous tissue above the general level of the zoecial secondary frontal walls. The extensive development of such tertiary frontal walls has no close parallel in Recent cribrimorph genera. Extensive olocystal or tremocystal skeletal thickening is achieved by some ascophoran bryozoans such as *Porina*, *Semihawwellia*, *Tremotoichos* and *Bathystomella*. The scale of this extra calcification is comparable with that of the tertiary frontal walls of some later Cretaceous cribrimorphs but its mode of formation is different.

. THE FUNCTION OF EXTRA FRONTAL CALCIFICATION

Variation and complexity of costate secondary frontal walls in Cretaceous cribrimorphs relates to the activity and function of individual zoecia, but elaborate subsequent calcification to form a tertiary frontal wall poses a problem of interpretation. It is difficult to understand how the formation of a robust outer layer of calcareous tissue can be related to polypide activity. The mode of secretion of

tertiary frontal walls, or even of lesser amounts of interzooecial tissue, is obscure and information is lacking on the relations of the calcareous skeleton to the secretory soft tissues in Recent bryozoans. However, some "mantle-like" extension of secretory soft tissue over the whole colony seems to be indicated by the tertiary frontal wall structures which were developed by many Cretaceous cribrimorphs.

Functionally, the significance of a well developed tertiary frontal wall would seem to relate to the colony as a whole rather than directly to individual zooecia. Its development affords protection for the more delicate subjacent costate frontal walls of zooecia and for their contained polypides. It acts as a coarse outer filter to the zoarium precluding penetration by larger organisms or by coarse detritus and it may even be effective in retaining a certain amount of graded detritus forming a further protection over the surface of the zoarium.

A similar interpretation could be made of frontal structures of some much less calcified Cheilostomata. The single lateral scute-like spines of *Canda clypeata* (Text-fig. 7) clearly relate to the individual zooecia which bear them, but in multiserial laminar zoaria the frontal spines of adjoining zooecia form in effect a continuous lattice over the whole zoarium and their function relates also to the colony as a whole. Recent species of *Hiantopora*—*H. ferox* (Text-fig. 8) and *H. intermedia* (Text-figs. 9, 10)—demonstrate the overgrowth of branched marginal spines in association with prominent avicularia combining to form a frontal shield over each zooecium. Since these shields are developed by adjacent zooecia they form a protective barrier for the whole colony and a filter in which the largest openings are located over the orifices of the zooecia. Other structures may also function in this fashion, for example, the abundant and very prominent branched oral spines of such Recent species as *Chaperia cervicornis*.



FIG. 8. *Hiantopora ferox*. Recent. Single adult zooecium with lateral avicularium.
B.M.(N.H.) Zool. Dept. 99.7.1.1371.

The Cretaceous species *Stichocados verruculosus* Marsson has similarly well developed large and robust oral spines and it is significant that the minute branched spines rising from the secondary frontal wall are sited adjacent to the largest openings in that structure.

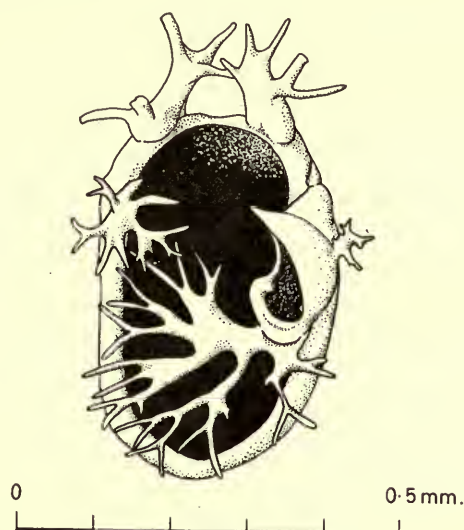


FIG. 9. *Hiantopora intermedia*. Recent. Single adult zoecium and an associated lateral avicularium. B.M.(N.H.) Zool. Dept. 28.3.6.52.

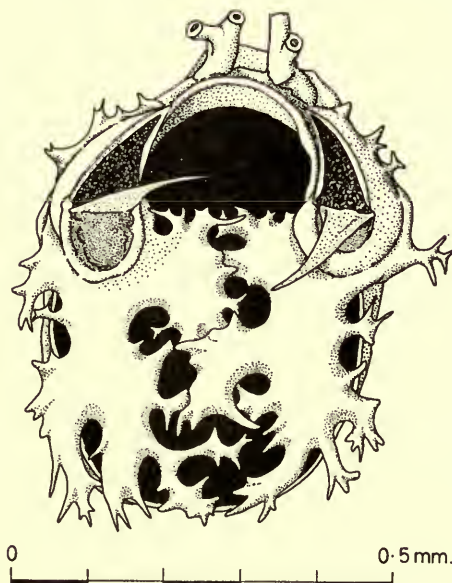


FIG. 10. *Hiantopora intermedia*. Recent. Single adult zoecium and paired oral avicularia. Note the robust development of frontal spines compared with those of the zoecium shown in Text-fig. 9. B.M.(N.H.) Zool. Dept. 28.9.13.22.

The complex tertiary frontal walls developed in Cretaceous cribrimorphs are a specialized example of a zoarial filter and protective lattice. Structures which are developed in relation to zooecial orifices and the variety of heterozooecia in the Cretaceous cribrimorphs are often incorporated into the secondary and tertiary frontal wall systems and will be considered elsewhere.

SUMMARY

The structure of the secondary frontal walls in some Cretaceous cribrimorphs is compared with that developed in the frontal walls of some Recent cribrimorphs. Cretaceous cribrimorph genera which develop tertiary frontal walls are considered and the function of extra frontal calcification generally is briefly discussed.

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THE MORPHOLOGY AND
SYSTEMATIC POSITION OF THE
ALEPOCEPHALOID FISHES

W. A. GOSLINE

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ZOOLOGY

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THE MORPHOLOGY AND SYSTEMATIC POSITION OF THE ALEPOCEPHALOID FISHES



BY

WILLIAM ALONZO GOSLINE

University of Hawaii

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By WILLIAM ALONZO GOSLINE

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INTRODUCTION

THE alepocephaloids are black, marine fishes living today in fairly deep to very deep water. Their maxillary is included in the gape, and they have no gas bladder and no adipose fin.

The group has received some, though by no means adequate, taxonomic attention in recent years. Parr (1951, 1952) provided preliminary accounts of the Alepocephalidae and in 1960 reviewed the related Searsidae (or Searsiidae; Parr's spelling of the family name will be used here). Marshall (1966) described the new family Bathypriionidae, and, on the basis of previous accounts, removed *Leptochilichthys* from the Alepocephalidae and erected a separate family, Leptochilichthyidae, for it. Most recently, Nielsen & Larsen (1968) have shown that the controversial Bathylaconidae (Parr, 1948) belongs with the alepocephaloid fishes.

Though the above five families appear to form a coherent, if varied, group of related fishes, their position in the Teleostei has remained obscure. Usually they have been treated as dubious relatives of the clupeoid or salmonoid fishes, but sometimes as a separate group, e.g., Marshall (1966). The basic difficulty has been a lack of knowledge concerning the internal structure of alepocephaloids. The most complete account of the osteology of the head remains that of Gegenbaur (1878) for *Alepocephalus rostratus*. Derschied (1924) described the nasal apparatus of the same species. Parr (1960) noted certain superficial head bones in some searsids. Gosline (1960) and Patterson (1968) have discussed and illustrated the caudal skeleton of *Alepocephalus rostratus* and Bonde (in Nielsen & Larsen, 1968) figured that of *Bathylaco nigricans*. Two illustrations of the head skeleton of *Bathypriion danae* by Bertelsen and a description and figure of some of the visceral organs of the same fish have been published by Marshall (1966). Nelson (1967), in a paper on epibranchial organs, has provided a figure of the posterior gill arch structure of *Alepocephalus macropterus*. McAllister (1968) summarized data on the branchiostegal rays of alepocephaloids. Greenwood et al. (1966: 373, 374) have reviewed most of what is known about the osteology of the group, adding certain items of information not to be found elsewhere.

In the present paper the osteology of *Alepocephalus rostratus* (Fig. 1) will be treated in detail. Though this species is probably a rather specialized alepocephaloid, it is the only one for which a specimen was available for staining and complete dissection. Comparative material used to a more limited extent included two skeletons of *A. rostratus* and preserved specimens of the alepocephalid *Xenodermichthys socialis* and the searsid *Searsia koefoedi* in the British Museum (Natural History); preserved specimens of the bathypriionid *Bathypriion danae* and the bathylaconid *Bathylaco nigricans* in the Zoological Museum in Copenhagen; and a preserved *Alepocephalus macrocephalus* at the University of Hawaii.

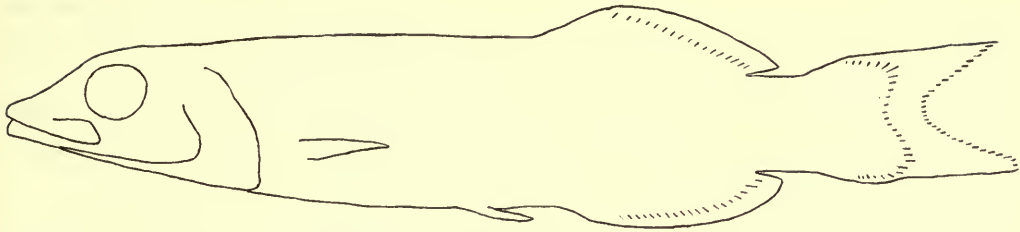


FIG. 1. Sketch of *Alepocephalus rostratus*, based on the 350 mm. specimen dissected.

MATERIALS AND METHODS

A single specimen of *A. rostratus*, 350 mm. in standard length, taken off the coast of Ireland ($52^{\circ} 06' N$ $12^{\circ} 27' W$) in about 380–455 fthms of water by Mr. A. Wheeler in July, 1968 was dissected. This specimen is part of the British Museum (Natural History) collections. The specimen was preserved in formaldehyde, and transferred to alcohol. For one day during the time it was soaking in water prior to placement in alcohol, a slight amount of potassium hydroxide and considerable alizarin solution was added to the water. This had the effect of staining all the superficial bones a dark red, the deeper bone pink, and some of the bony elements most deeply embedded in flesh, e.g., the intermuscular bones, not at all.

There are certain advantages and disadvantages to this method of preparation. In the first place, with a skeleton as largely cartilaginous as that of *Alepocephalus*, a dried skeleton shrivels considerably. As compared to a clearing and staining technique, the method used here (assuming that the fish had been left in stain longer and that the stain had penetrated better) has advantages and disadvantages. In the first place, there is perhaps some question whether a fish of 350 mm. could be adequately and feasibly cleared. Second, the specimen used here is far easier to work with than one in glycerin. During dissection it was merely covered with a wet rag (though this did not altogether prevent shrinking of the cartilage). Third, the muscles and their attachments and, to some extent, the lateral line canals were easier to see than if the specimen had been cleared. The great disadvantage of the present technique lies in the fact that in the vertebral column and related bones, each item, e.g., intermuscular bone, has to be dissected individually. This is not only tedious, but there is always the possibility of losing elements during dissection. For the determination of ribs and intermuscular bones and their relationships a cleared and stained specimen is far better.

ABBREVIATIONS USED IN FIGURES

Ac	actinost	bl	Baudelot's ligament
ah	articular head	Bo	basioccipital
Al	autopalatine	Br	branchiostegal ray
An	angular		
Ao	antorbital	ca	cartilage
Ap	autopterotic	Cb	ceratobranchial
Ar	articular	Cl	cleithrum
As	autosphenotic	cn	cartilaginous nodule

Co	coracoid	mp	superficial epaxial musculature to post-temporal
De	dentary	Ms	mesopterygoid
Dl	dermopalatine	Mt	metapterygoid
Dp	dermopterotic	mu	median band of musculature to supra-occipital
Dr	dorsal ray	Mx	maxillary
Ds	dermosphenotic		
		Na	neural arch
Eb	epibranchial	Ns	neural spine
Ec	ectopterygoid		
El	epipleural	Op	opercle
em	epaxial musculature	or	orbit
En	epineural		
Ep	epiotic	Pa	parietal
Es	extrascapular bone	Pd	predorsal bone and cartilage
Et	ethmoid bone	Pe	uppermost pectoral ray
Ex	exoccipital	Pl	pleural rib
		Pm	premaxillary
Fr	frontal	Po	posttemporal
		Pp	preopercle
gr	groove for attachment of the adductor hyomandibulae	Pr	prootic
		Ps	parasphenoid
hm	hypaxial musculature	Qu	quadrate
hs	socket for hyomandibular articulation		
Hy	hyomandibular	Ra	radial
Ib	infrapharyngobranchial	Sa	sesamoid articular
Io	interopercle	Sb	suprapharyngobranchial
		Sc	scapula
Le	lateral ethmoid	Sl	supracleithrum
li	ligament	So	supraorbital
Ll	lateral line ossicle	Sp	subopercle
ll	lateral line to body	ss	suspensorium
lp	ligament to posttemporal	Su	supraoccipital
		Sy	symplectic
ma	lateral epaxial muscle to autopterotic	tf	lateral exit of trigemino-facialis nerve complex
mc	Meckel's cartilage		
me	deeper epaxial musculature to epiotic, etc.	va	exit for vagus nerve
Mo	mesocoracoid	Vc	vertebral centrum

THE OSTEOLOGY OF ALEPOCEPHALOID FISHES WITH PARTICULAR
REFERENCE TO *ALEPOCEPHALUS ROSTRATUS*

Bone formation

Alepocephalus rostratus is weakly calcified. The dermal bones of the head, which stain the most deeply in alizarin, are thin sheets easily stripped off from the underlying chondrocranium (Gegenbaur, 1878). In the skull much cartilage is retained. At least in the front of the vertebral column the centra do not appear to be ossified; nevertheless, the fact that their identity remains in a dried skeleton suggests that

they are fibrous rather than cartilaginous. The endochondral bones of the skull are opaque, like the cartilage, and take up very little alizarin. As Gegenbaur (1878) pointed out, the endochondral bones show concentric markings, suggesting growth rings. However, in the 350 mm. specimen of *A. rostratus* most of the endochondral bones remain separated from one another by cartilage.

The dermal bones, as suggested, are fragile and easily fractured. Such fracturing apparently occurs frequently in life. The extent of dermal ossification also seems to vary considerably among species of alepocephaloids. Thus, in *A. rostratus* the lateral ethmoid is a small, completely endochondral bone completely surrounded by cartilage (Fig. 4, Le), but in some searsids it forms a significant portion of the skull roof (see Parr, 1960) and is probably capped by dermal bone. Again, the circum-orbital bones, aside from the lacrimal, may be reduced to tubular ossicles, as in *A. rostratus*, or expanded into plates in some searsids.

It may well be that the unusually poor calcification of the *Alepocephalus* skeleton serves as a partial density compensation for the lack of a gas bladder (Denton & Marshall, 1958). In any event, the dried skeletons of *Alepocephalus rostratus* are very light in weight.

The sensory systems and associated ossifications

Alepocephalus rostratus has a very large eye (Fig. 1) and a well-developed olfactory rosette; on the other hand the lateral line canals of the head, particularly on the dorsal surface of the head, are fragmented, reduced in size, and apparently without open pores. However, in such a fish as *Bathyprion danae* (Marshall, 1966, fig. 1) the eyes are small, and in *Searsia koefoedi* the lateralis system of the head is expanded as a series of arborescent tubules, each ending in an open pore. Thus the alepocephaloids as a whole can hardly be characterized in terms of any particular sensory development.

The olfactory apparatus. The nasal apparatus of *Alepocephalus rostratus* has been described and figured by Derschied (1923, pp. 115-118, fig. 11). The anterior and, especially, the posterior nostrils are ample holes without bordering collars separated by a bridge of skin. These lead into a large, simple nasal cavity most of which lies anteroventral to the nasal openings. In the posterodorsal portion of this cavity and below the nasal openings lies a typical but well-developed nasal rosette.

The antorbital-supraorbital strut, used by so many isospondylous fishes as a method for pumping water in and out of the nasal cavities and hence across the nasal epithelium (Derschied, 1923; Gosline, 1961; Kirkhoff, 1958) does not occur in *Alepocephalus rostratus*. There is no supraorbital bone in this fish, and the antorbital is a weak L-shaped splint lying free in the skin. (In *A. macropterus* both the supraorbital and antorbital bones are absent.) Nevertheless, it seems probable that the nasal sac of *Alepocephalus rostratus* is expanded when the mouth is opened and contracted when the mouth closes. A short, strong ligament from the forward portion of the lacrimal (or a pre-lacrimal ossicle, see below) extends anteriorly to an attachment on the top of the maxillary, so that movement of the maxillary must change the position of the lacrimal. In the preserved specimen at hand, the skin

over the nasal sac is somewhat concave when the mouth is closed, but is drawn taut when the posterior end of the maxillary is moved downward.

Though the method for pumping water over the olfactory rosette is somewhat different from that of most lower teleosts, I think this difference can be sufficiently explained by the exigencies of the relatively long, rather ski-jump shaped snout of *A. rostratus* (Fig. 1).

In contrast with the alepocephalids described above, there appears to be on one side of a relatively undamaged specimen of *Bathylaco nigricans* the usual isospondylous antorbital-supraorbital strut (see Fig. 6c). In view of the shorter snout of *Bathylaco*, as compared with *Alepocephalus*, a more normal olfactory apparatus might be expected.

The lateralis system of the head. The infraorbital canal of *Alepocephalus rostratus* commences at the front of the lacrimal in an upturned tubule. In some specimens this upturned tubule occurs in a separate ossification, but this separate element would seem to be a broken piece of the lacrimal rather than an independent rostral bone. I can find no continuation of this upturned tubule in the skin of the snout or in the dermal portion of the median ethmoid bone. Behind the lacrimal, the infraorbital canal continues around the eye in a series of weak, tubular ossicles, seven on one side and eight on the other. The central ossicles of this series have slight laminar bases but the terminal ones do not. Behind the eye these ossicles are well separated from the orbital border, with cheek musculature extending forward below them. The uppermost (dermosphenotic) is loosely attached to the autosphenotic by membrane. Above the dermosphenotic the infraorbital canal is continued as a membranous tube which barely meets the tip of a forward projection, also in a membranous tube, of the temporal canal. The infraorbital system of *A. rostratus* has been adequately illustrated by Gegenbaur (1878, pl. 2, fig. 8).

The supraorbital canal begins at the front of the very long nasal bones, which are primarily tubular and lie alongside the upper portion of the ethmoid region of the skull. After a hiatus between the nasal and frontal bones, the canals continue to the back of the frontals, where they end.

The mandibular-preopercular canal runs its usual course from the front of the dentary to a tubular extension from the top of the preopercle. From there it proceeds via a membranous extension to a junction with the temporal canal. There is no supraperopercular ossification.

The temporal canal extends back in the dermopterotic to a point just anterior to the preopercular canal where it drops down to a Y-shaped junction with that canal, thence back up again into a short section of the dermopterotic and out the rear of that bone. From the membranous section of the temporal canal behind the dermopterotic the supratemporal commissure extends at right angles over the skull roof. The supratemporal commissure is mostly contained in two small, tubular ossicles (see Fig. 9, Es) before ending blindly. The lateral of these two ossicles is underlain by a fleshy area, but the medial overlaps the parietal from which it is separated by membrane.

From behind its junction with the supratemporal commissure the temporal canal passes back through a small, straight, tubular ossicle and then through an ossicle

movably attached to the base of the posttemporal (Fig. 9, Ll). In this ossicle the canal forms a downward bend, passing thence along the supracleithrum and out onto the body (Fig. 12, ll). The fact that the lateralis and dermal components are separate in the posttemporal (but not in the supracleithrum) in *A. rostratus* is peculiar, perhaps significant.

The relative expansion of the lateralis system in *Searsia koefoedi* as compared to *Alepocephalus rostratus* has already been noted. In *Searsia koefoedi*, the supra-orbital canal is continuous from the nasals through the frontals to a posterior junction with the canals of the supratemporal commissure. In *S. koefoedi* I can find no ethmoidal or frontal commissure, there is no junction of the infraorbital and supra-orbital canals, and the supratemporal canals of the two sides do not meet on the middorsal line. Nor have I observed any of the features mentioned in the last sentence in other alepocephaloids. So far as the systematic position of the alepocephaloids is concerned, the lack of an ethmoid commissure and the failure of the infraorbital and supraorbital canals to meet would seem to be the most significant features of the lateralis system of the head.

The jaws and jaw mechanisms

The lower jaw is long in *Alepocephalus rostratus*. It retains three areas of cartilage on its inner face (Fig. 2). Two of these are associated with the articular (angular of

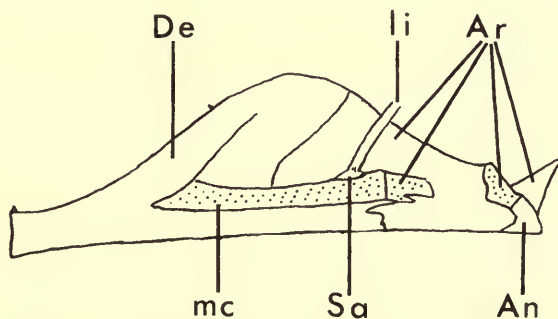


FIG. 2. Right mandible of *Alepocephalus rostratus*, internal view. Only the anteriormost and posteriormost teeth are indicated. Cartilage stippled.

Haines, etc.). One extends upward and forward from a lobe on the angular to the base of the articular-quadrate junction. The other is the endosteal process of Starks (1916, p. 6) which extends forward to Meckel's cartilage. The latter is a strut, somewhat thicker at the two ends, extending between a posterior abutment against the endosteal process of the articular and a forward enclosure by the dentary. The sesamoid articular (Fig. 2, Sa) is a small bone on the upper surface of Meckel's cartilage; it has no other attachment and nowhere meets the articular in the undried fish.

The mouth is closed by means of contraction of the adductor mandibulae. The adductor has its insertion on the inner surface of the articular with a major concen-

tration of musculature attached by ligament (Fig. 2,li) to the sesamoid articular. Posteriorly, the adductor originates on the outer surface of the suspensorium. The surface of attachment extends across the quadrate and the lower portion of the metapterygoid onto the hyomandibular; there is very little attachment surface on the opercle.

The apparatus for lowering the mandible of *Alepocephalus rostratus* is peculiar. Not one but rather two separate ligaments are attached to the rear of the angular. The upper of these passes directly up and back to an attachment on the outer face of the epihyal. The lower of the two passes back to an attachment near the front of the interopercle, along the upper, inner face of that bone for a short distance, and then leaves it to pass inward and upward to an attachment on the outer surface of the epihyal just below that of the upper angular-epihyal ligament. Posteriorly, the interopercle of *Alepocephalus* has a well-defined membranous attachment to the subopercle which in turn is closely attached by membrane to the under surface of the opercle. The upper surface of the opercle in turn has a well-developed levator operculi muscle which extends anterodorsally to an attachment on the pterotic. It therefore seems that contraction of the levator operculi would serve to lower the mandible as described by van Dobben (1935) by pulling back on the lower of the two ligaments to the angular. It also appears that backward or outward movement of the epihyal would accomplish the same thing (Kirkhoff, 1958 : 524) by a backward pull on the upper of the two ligaments to the angular. This double mechanism for opening the mouth seems to be normal in living lower teleosts; at least I have found variants of it in *Elops*, *Albula*, *Chanos*, *Osmerus*, *Salmo*, *Chirocentrus*, and *Clupea*.

In the holostean *Amia* there is a single strong ligament (lmh of Allis, 1897, pl. 19, fig. 2) extending freely between the interopercle (externally) and the outermost branchiostegal ray (internally) to an attachment on the outer face of the epihyal. The forward end of the interopercle is merely attached by loose membrane to the articular area of the mandible above the angular, whereas the outermost branchiostegal ray is equally firmly attached to the articular area of the mandible below the angular. In *Amia*, then, the interopercle has no special attachment to the mandible and none whatever to the angular; it appears to act merely as the uppermost member of the branchiostegal series (McAllister, 1968 : 4).

It would seem, from the condition described in *Amia*, that (1) retraction or expansion of the rear portion of the hyoid arches plays the primary role in lowering the mandible of that fish, (2) that the angular may have arisen as a source of attachment for the epihyal-angular ligament, and (3) that the interopercle can have little to do with the opening of the mouth. From this it appears probable that the incorporation of the interopercle into the mechanism for opening the mouth has arisen in the Teleostei, either by attachment of the interopercle to all or to a portion of the angular-epihyal ligament. *Alepocephalus* differs from other teleosts investigated in having the angular-epihyal ligament divided into two completely separate parts, one attached to the interopercle and one not. In this separation *Alepocephalus* only differs in degree, however, from the condition seen in *Osteoglossum*, and for that matter from other lower teleosts.

Among the various alepocephaloids the ligamentous attachment of the angular and the mechanism for opening the mouth differ among the forms examined. *Bathylaco* shows the typical teleostean condition with a single ligament extending back to the interopercle. *Alepocephalus rostratus* shows the double attachment already noted. *Xenodermichthys socialis* shows a further specialization of the *Alepocephalus* condition in that the subopercle has become reduced to a small strut that does not meet the interopercle at all (Fig. 3A). In this fish, as in *Amia*, the interopercle cannot serve as a mechanism for lowering the mandible. However, the opercular apparatus of *Xenodermichthys* is of a highly specialized construction, presumably arising from an *Alepocephalus*-like opercular type, and is hence most probably a secondary development within the alepocephaloids. A far more normal type of opercular apparatus, differing from that of *Amia* most significantly in the presence of an angular-interopercle ligament, is that found in *Searsia koefoedi* (Fig. 3B).

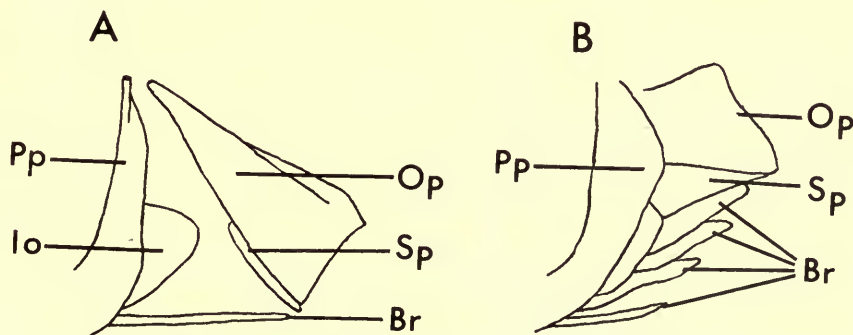


FIG. 3. Left gill cover, external view, of (A) *Xenodermichthys socialis* and (B) *Searsia koefoedi*.

The upper jaw of *Alepocephalus rostratus* consists, on each side, of a short premaxillary, a much longer maxillary, and two supramaxillaries. The premaxillary and maxillary bear short teeth. The maxillary has two articular facets, both on its mesial surface anteriorly. The forward of these props the maxillary against the ethmoid cartilage and the posterior against the cartilaginous tip of the autopalatine (Fig. 4A). Anterior to its front articular facet, the maxillary thins into a vertically flattened wedge extending somewhat between the premaxillary and the ethmoid.

In the alepocephaloids examined, the condition of the premaxillaries varies considerably. Among certain searsids, at the one extreme, the premaxillaries form a sort of a cap over the front of the snout, and have forwardly projecting tusks (see Parr, 1960). At the other, represented by *Bathypriion*, the ethmoid region projects well forward of and between the premaxillaries (Marshall, 1966).

In *Alepocephalus rostratus* the posterior end of the maxillary is membranously connected with the outer surface of the mandible, and when this is lowered the lateral end of the maxillary moves down with it. Stretching of the maxillary-mandibular membrane when the mouth is opened also has the effect of pulling

upward the anterior end of the posterior supramaxillary in typically "clupeoid" fashion.

There is also a long ligament (Fig. 4A) extending back from the outer surface of the maxillary anteriorly into the membrane attached to the lower jaw. When the mandible is lowered the shortening of this ligament presumably rolls the lower edge of the maxillary outward (van Dobben, 1935).

Lowering and rolling of the maxillary must transfer some motion of the same sort to the premaxillaries. In addition to the usual (but rather tight) membranous attachment of the premaxillaries to the ethmoid block anteriorly, there are ligaments extending from the fronts of ridges running anterolaterally on each side of the ethmoid to the lateral portions of the premaxillaries (Fig. 4A); these ligaments would prevent lowering of the premaxillaries but would permit an outward rolling of their lower rims.

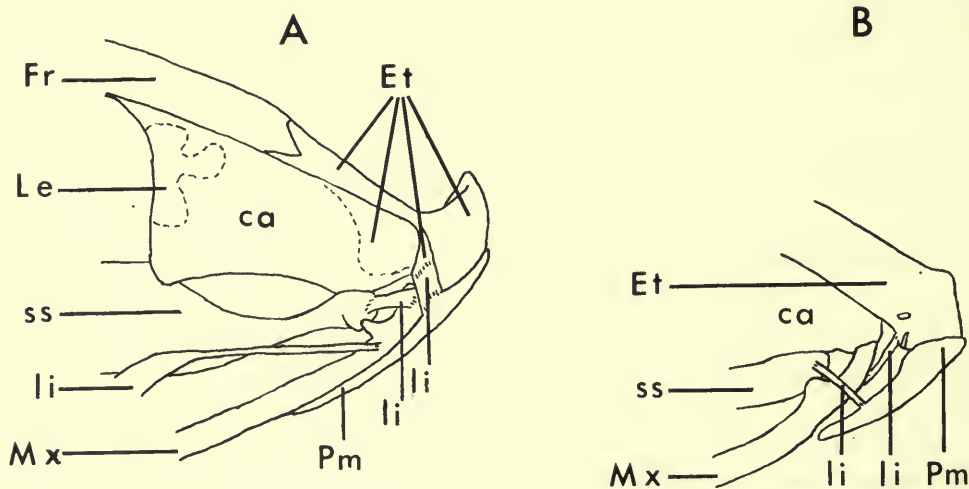


FIG. 4. Lateral and slightly superior views of the ethmoid region and forward ends of the suspensorium and upper jaw bones of (A) *Alepocephalus rostratus* and (B) *Elops saurus*.

The ligaments that extend from the lateral ridges of the ethmoid out onto the upper surface of the lateral portion of the premaxillaries must also serve the function of holding in place the maxillary heads, for these extend forward to this point between the ethmoid and the premaxillaries. Additionally, there are ligaments from the maxillary heads to the palatines (Fig. 4A). However well this system may serve *Alepocephalus*, it is the reverse of the usual system of ligaments in teleosts, where that from the palatine to the premaxillary crosses over another from the ethmoid to the maxillary (see, for example, Gosline, 1961, fig. 8c and p. 32).

The origin of these crossed ligaments can I think be traced back via *Elops* and *Megalops*. In *Alepocephalus* the tough, membranous tissue between the premaxillary and maxillary extends forward to the ethmoid. In this area in *Elops* (Fig. 4B) there is a tendon which, however, extends between the premaxillary and maxillary out

to an eventual attachment on the lower surface of the maxillary. This I think is the ethmoid-maxillary ligament of higher teleosts, the ethmoid-premaxillary ligament of *Alepocephalus* having disappeared. In *Megalops* the ethmoid-maxillary ligament is present, but in addition the premaxillaries have developed dorsal laminae which extend farther up over the rostrum than the premaxillaries of *Elops*. As a result a lateral portion of the premaxillary dorsal lamina is almost in contact with the outer surface of the palatine head, and a strong membrane or ligament is present between them. If this is the correct source for the palatine-premaxillary ligament (Fig. 4B), it has no homologue in *Alepocephalus*. Whether other alepocephaloids have such a ligament I was unable to determine.

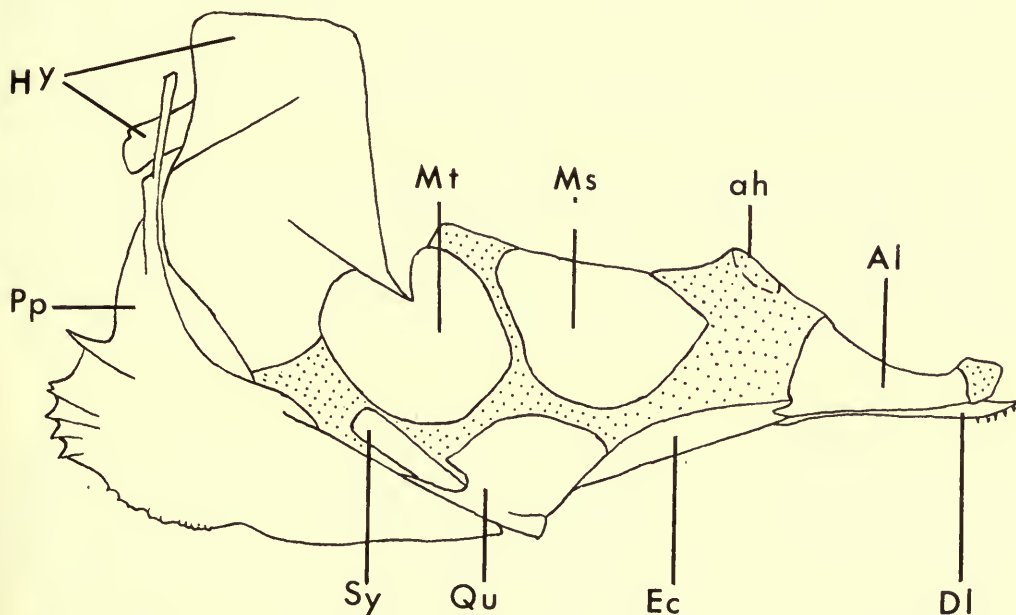


FIG. 5. External view of right half of suspensorium of *Alepocephalus rostratus*. Cartilage stippled.

The suspensorium

The autopalatine and (toothed) dermopalatine are represented by separate bones in *Alepocephalus rostratus* (Fig. 5). The dermopalatine is merely a toothed plate which extends inward beyond the autopalatine to nearly meet its fellow on the midline. The autopalatines are continued forward by a nodule of cartilage which extends between the ethmoid block and the articular head of the maxillary (Fig. 4A).

The anterior end of the ectopterygoid wedges slightly between the posterior ends of the dermopalatine and the autopalatine. The large mesopterygoid is toothless and completely surrounded by cartilage. Its upper edge extends inward nearly to the parasphenoid; this edge is continued posteriorly by a squarish cartilaginous lamina. The metapterygoid is a circular bone with a deep wedge missing. Anterior to this wedge, the metapterygoid forms a continuous, more or less horizontal surface

with the infolded mesopterygoid. Posterior to the wedge the metapterygoid forms a continuous vertical surface with the hyomandibular. The hyomandibular articulates with the cranium by a single, broad head. Posteriorly it gives off a long strut against which the operculum articulates.

External to its hyomandibular articulation, the operculum has a bony flange which serves for the attachment of the dilatator operculi muscle. This muscle extends forward and upward to an attachment on the pterotic. The elevator operculi extends from the upper surface of the operculum upward to an attachment on the pterotic behind the dilatator operculi.

Perhaps the most notable feature about the suspensorium of *Alepocephalus rostratus* is the separate autopalatine and dermopalatine. This occurs elsewhere among living teleosts only, to my knowledge, in the elopoids (Gosline, 1961). Possibly, however, this separation of the two palatine elements in *Alepocephalus* has developed secondarily in association with the general reduction in ossification in this fish.

Alepocephalus rostratus has no basipterygoid process, though the block of cartilage posterior to the mesopterygoid suggests the rudiment of such a process. In *Searsia koefoedi* there is a single row of large, well-spaced teeth on the inner border of the mesopterygoid, and the cartilaginous area behind the mesopterygoid appears to be propped against (or perhaps between) a pair of knob-like projections from the parasphenoid. In short, *Searsia koefoedi* appears to have a basipterygoid process.

The cranium

Rostral region. The rostrum of *Alepocephalus* consists primarily of cartilage (Gegenbaur, 1878, pl. 1, fig. 5). At its flattened tip the snout forms sort of a sandwich of cartilage between two dermal bones—a dermethmoid above and the vomer below. The dermethmoid lies entirely superficial to the cartilage. Possibly the posterolateral portions of the ethmoid ossification, included in the dashed line in Fig. 4A, represent an endochondral element, for they contain no superficial irregularities and stain less deeply than the central portion, but they, too, merely form a thin cap over the ethmoid cartilage below. Posterodorsally the dermethmoid interdigitates with the anterior end of the frontals. The front of the median, toothless vomer extends almost to the snout tip at the midline. More posteriorly it spreads out as a thin, flat plate on the lower surface of the ethmoid cartilage, passing back ventral to the parasphenoid. The anterior ends of the dermopalatines swing medially below the vomer. However, the cartilaginous anterior tip of the autopalatine articulates with the ethmoid cartilage above and lateral to the vomer.

Posteriorly the ethmoid cartilage forms two vertical, lateral struts. Embedded in these, and reaching neither the frontals above nor the parasphenoid below, are the completely endochondral lateral ethmoids (Fig. 4A). Each lateral ethmoid above borders the opening through which the olfactory nerve passes.

The lower surface of each lateral strut forms a cartilaginous facet for the articulation of the cartilaginous upper surface of the suspensorium between the autopalatines and the mesopterygoid (Fig. 5,ah).

The posterior faces of the lateral cartilaginous struts form the anterior borders for the eyeball. On the midline the cartilaginous ethmoidal block extends somewhat posteriorly to the lateral flanges. This median area contains two anterior myodomes, one above the other. Between the two, the cartilage projects posteriorly and forms the surface for attachment of a median, ligament-like membrane that extends up and back to a forward projection of the median orbitosphenoid.

Skull roof. The skull roof of *Alepocephalus rostratus* has been illustrated by Gegenbaur (1878, pl. 1, fig. 3) and this figure appears redrawn in Gregory (1933, fig. 51). Unfortunately it is badly in error with regard to the bones on the parietal-epiotic region.

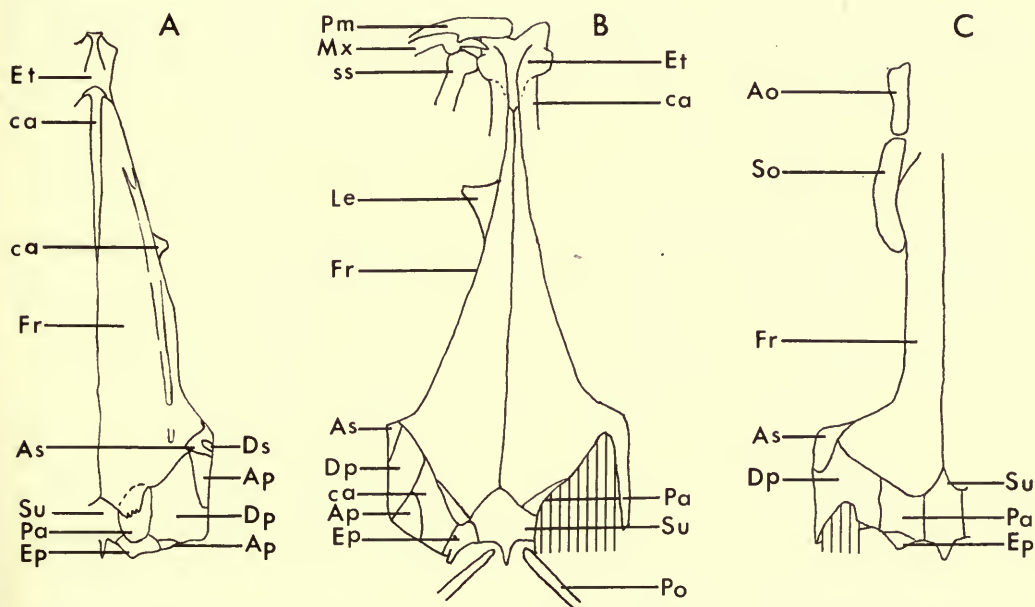


FIG. 6. Skull roofs, from above, of (A) right half of *Alepocephalus macropterus*, with the course of the lateral line indicated; (B) *Xenodermichthys socialis*, with the forward ends of the left suspensorium and upper jaw bones and the posttemporals shown; and (C) the left half of *Bathylaco nigricans* with the approximate position of the presumed antorbital-supraorbital strut indicated. The forward ends of the epaxial musculature are shown by parallel lines on the right half of (B) and in (C).

The frontals are much the largest bones on the skull roof (Fig. 6). At the back of the orbital rim they slightly overlap the upper portion of the autosphenotic. More posterolaterally the frontals form a continuous border with the dermopterotics. Posteriorly the frontals overlap the parietals and supraoccipital.

The dermopterotic of *Alepocephalus* is a thin sheet of bone overlapping, but separate from the autopterotic. Aside from the frontals the dermopterotics are the largest bones on the skull roof. Anteriorly, they extend over the autosphenotics. Laterally, they extend to the posterolateral angle of the skull roof, though ahead of that a small part of the autopterotic, above that portion that forms the posterior

half of the hyomandibular facet, is exposed (Fig. 6A,Ap). (The autopterotic also extends somewhat behind the level of the dermopterotic on the posterior face of the skull.) Medially, the dermopterotics border the frontals and parietals.

The supraoccipital, though quite small, completely separates the parietals. It has three short, parallel ridges on its dorsal surface, which presumably represent a dermal component. The parietals extend under the frontals anteriorly and over the epiotics posteriorly. The epiotics, despite Gegenbaur and Gregory (see above), do not form part of the skull roof though they protrude somewhat posteriorly on the posterior face of the cranium.

The floor of the cranium. The parasphenoid is a long bone, passing between the vomer and the ethmoid cartilage forward and extending under the basioccipital posteriorly (Fig. 7). Under the posteroventral border of the orbits, there are slight dorsolateral flanges on the parasphenoid that extend out in front of the prootics.

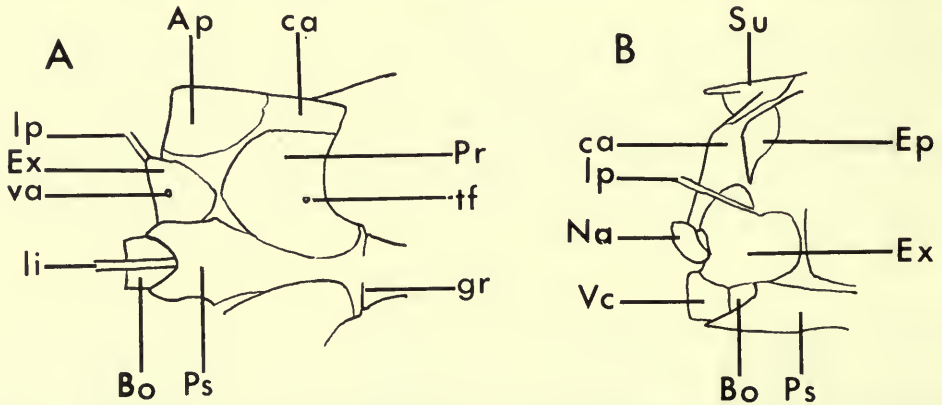


FIG. 7. Posterior portion of right half of cranium of *Alepocephalus rostratus* from (A) below, and (B) the side.

On the ventral surface of these flanges there is, on each side, a groove (Fig. 7A,gr) that extends at right angles to the longitudinal shaft of the parasphenoid. These grooves serve for the attachment of muscles which, on contracting, pull the suspensorium in toward the parasphenoid. Posteriorly, a ligament issues from the space between the parasphenoid and the basioccipital and passes back below the vertebral column (Fig. 7A).

Sphenoid region. Posteromedially the orbits are bordered by the median orbitosphenoid and the paired pterosphenoïds (Gegenbaur, 1878, pl 1, fig. 4). The olfactory nerves pass forward from a median hole between the front end of the orbitosphenoid, which is V-shaped in cross section, and the cartilage above it. The endochondral pterosphenoïds meet one another below anteriorly but not posteriorly. Anteriorly the pterosphenoïds meet the orbitosphenoids. Above they meet lightly ossified flanges of the frontals which extend down over much of the posterodorsal surface of the orbit. Posterodorsally each pterosphenoïd is separated from the sphenotic by cartilage; posteriorly it nearly meets the prootic; and posteroventrally it is slightly separated from the wing of the basisphenoid. The basisphenoid wings, which meet

one another on the midline, seem to form the principal sources of attachment for two of the eye muscles. The basal median strut of the basisphenoid appears to be variously developed in different specimens of *Alepocephalus rostratus*. Gegenbaur (1878) describes and figures a rather well-developed median strut. A similar strut seems to be represented in the two prepared skeletons available. However, in the wet specimen I can find only an unossified ligament where the strut should be.

Otic region. The autosphenotic is a relatively large bone at the posterodorsal corner of the orbital border. Above and anteriorly it is overlapped by the frontal. Posteriorly it meets the autopterotic. Below, it extends to the upper border of the anterior portion of the socket for the hyomandibular articulation. The socket itself is cartilaginous anteriorly (Fig. 8,hs).

The prootic forms the lower border of the anterior portion of the socket for the hyomandibular. Anteriorly it extends into the orbit, bordering both the pterosphenoids and the basisphenoid. The trigeminal-facialis nerve has a single opening in the orbital face of the prootic, then a branch passes through a hole in the rim to exit on the lateral face of the same bone (Fig. 7A,tf). Ventrally the prootic meets the parasphenoid.

The posterior face of the skull. The supraoccipital does not extend down far on the posterior face of the skull, so that the central section down to the border of the foramen magnum is cartilaginous (Fig. 7B). The rims of the foramen magnum are bordered anterolaterally by the exoccipitals. These have no facets for vertebral articulation. However, they have lower facet-like projections into the upper surface of a part of the posterior portion of the basioccipital (?) that looks very much like an anterior vertebra that has become fused to the skull (Fig. 7B,Vc). Ridewood (1904, p. 64) notes this same inclusion of a half vertebra into the basioccipital of *Amia* and *Megalops*. Posterolaterally the foramen magnum is covered on either side by small, separate plates (Fig. 7B,Na) that doubtless represent the neural arches of the centrum that has become fused to the skull.

There are no fossae of any sort on the posterior or inferior faces of the skull. The inferior face of the exoccipital is, however, evenly concave forming a shallow cavity into which the large mass of hypaxial muscle fits (Fig. 8).

Attachments of body musculature to the skull

Hypaxial musculature in Alepocephalus rostratus. In *Alepocephalus rostratus* a large mass of hypaxial body musculature extends forward underneath the cranium on either side of the parasphenoid (Fig. 8). The attachment surface for this musculature is made up principally by the exoccipitals medial to the exit of the vagus nerve and the whole posterior portion of the prootic. The vagus nerve, after exiting from the exoccipital (Fig. 7A,va), passes laterally over the dorsal surface of this musculature, thence downward over its surface.

I can find no comparable expansion of musculature under the skull of other fishes, though I have not examined other deep water forms where, possibly, it is an adaptive feature. In the holostean *Amia* a similar muscle extends in over the lower surface of the skull. It extends forward slightly over and slightly under the vagus nerve

(Allis, 1897, e.g., pl. 12, fig. 35). Ventrally this muscle in *Amia* extends forward onto the cartilage slightly ahead of the basioccipital, but ends far short of the prootic.

Among the teleosts examined, the elopoid *Albula* and the salmonoids *Argentina* and *Salmo* have this muscle extending forward on the lower surface of the skull about as in *Amia*. In the gonorhynchoid *Chanos* there seem to be several ligaments passing forward onto the under surface of the cranium but no musculature. In the elopoid *Megalops*, the body musculature to the lower face of the skull is restricted anteriorly to the area behind the gas bladder diverticula but expanded laterally as in *Alepocephalus*. In the clupeoid *Clupea* there is a very slight sheath of musculature extending outside of the gas bladder extension to an attachment on the skull anterior to the diverticulum; behind the diverticulum the attachments to the skull are principally ligaments with a slight amount of musculature interspersed.

From a priori considerations it seems that large muscle masses to the under surface of the skull and a connection between the gas bladder and the inner ear could not

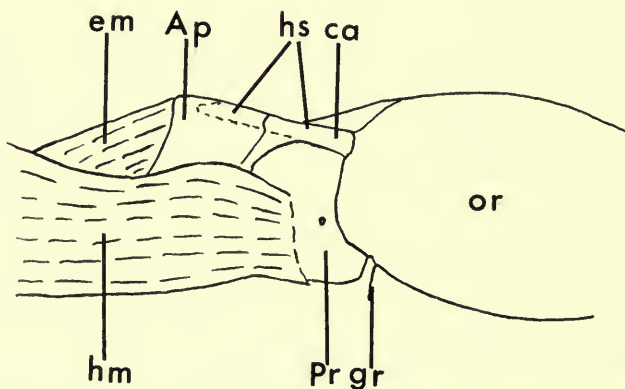


FIG. 8. Attachment of the body musculature, indicated by dashed lines, to the right half of the skull of *Alepocephalus rostratus*, from below.

effectively occur in the same fish. Possibly the great expansion of the hypaxial musculature to the skull in *Alepocephalus* is related to its loss of a gas bladder.

Epaxial musculature in Alepocephalus rostratus. The relationship between the body musculature and the top portion of the cranium is more complicated (Fig. 9). Starting on the midline, the supraoccipital furnishes attachment for ligamentous tissue which leads into a band of musculature extending down the midline of the back (Fig. 9, mu). The dorsal wing of the posttemporal extends in over the dorsal surface of the nape almost to the supraoccipital. It has no direct articulation with the cranium; however, there is a strong ligament passing laterally from its tip to the posterodorsal surface of the epiotic. The attachments to the posterior edge of the posttemporal wing are of two types. Medially a ligament passes back into musculature which joins mostly the middorsal band but partly the epaxial body musculature. More laterally the posttemporal forms a rim for attachment of a thin sheet of epaxial body musculature (Fig. 9, mp).

Extending forward below the sheet of epaxial musculature to the posttemporal is another section of epaxial musculature that attaches to the back of the skull (Fig. 9,me). This portion passes in below the posttemporal-epiotic ligament medially but also around the epiotic end of this ligament to an attachment somewhat farther forward on the skull roof, just about reaching to below the lateral extrascapular (Fig. 9).

The deep fork of the posttemporal, continued as a ligament to the exoccipital (Fig. 7,lp), divides this portion of the epaxial musculature from a still more lateral portion which passes forward external to the deep fork to an attachment on the posterolateral face of the cranium (Fig. 9,ma). (This lateralmost portion also has a strong membranous connection to the inner surface of the posterolateral end of the posttemporal.) Anteriorly this lateral portion extends forward below the level of the main portion of the lateral line to an attachment on the cranium only slightly ahead of the level of the extrascapular ossicles (Fig. 9).

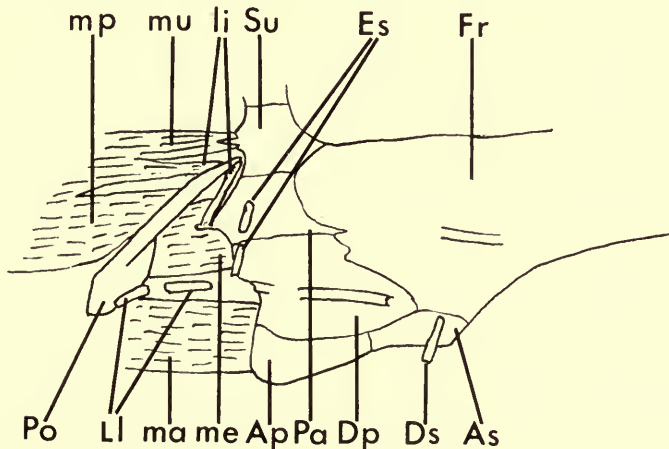


FIG. 9. Attachment of the body musculature, indicated by dashed lines, to the skull and posttemporal bone of the right side of *Alepocephalus rostratus*, from above.

The forward portion of the epaxial musculature can thus be divided into three parts depending on their relations to the posttemporal: (1) a superficial sheath attached to the upper wing of the posttemporal, (2) a deeper medial portion passing to the skull below the upper wing of the posttemporal and internal to its deep strut, and (3) a lateral portion passing forward to the skull external to the deep wing of the posttemporal. All three of these portions merge posteriorly into the epaxial body musculature.

The relationship between body muscle attachments and skull bones in actinopterygian fishes. In *Alepocephalus rostratus*, as already noted, there is no posttemporal fossa and very little epaxial musculature passing forward over the skull roof; on the other hand this fish has a great mass of hypaxial musculature extending far in under the floor of the skull. This is a most unusual, perhaps unique, arrangement. However, the nature of the skull bones to which the body muscles are attached varies considerably among alepocephaloids. Before dealing with these it seems well to review

the history of body muscle attachments to the skull in actinopterygian fishes.

In actinopterygians there has been a progressive specialization in the attachment of the body musculature to the cranium. For one thing, the cranium of higher forms provides greater and firmer sources of muscle attachment than in lower forms. For another, a specialization among the muscles attached to the skull seems to have developed.

In the higher actinopterygians, at least, there seems to be a relationship between concentrations of muscular stress and bone formation, as Gegenbaur (1878) pointed out long ago. Thus in *Amia* the main stress of muscular pull on the head appears to be concentrated into ligaments attached to the epiotics. This is not to say that all muscles attach to bone. Indeed, in *Amia* there are well-developed posttemporal fossae enclosed primarily by cartilage, and muscle attachment is distributed evenly over its surfaces. It is perhaps significant in this regard that the muscle attachments to the walls of the posttemporal fossae of *Chanos* are similar to those of *Amia* but that in *Chanos* an ossified ligament develops in the shaft of the musculature entering the fossa.

An increase in the surface for muscle attachment on the back of the skull in actinopterygians may take place in two ways: (1) by the extension of musculature into fossae in the skull or extension of the body muscles onto the horizontal surfaces of the skull or (2) by backward projections from the skull. The second method of increasing the surface of musculature attachment is well exemplified by the long terminally-frayed projections of the epiotics extending back into the body in *Sphyræna* (Starks, 1899), but occurring in numerous other fishes (see, for example, Ride-wood, 1904, pp. 65-66). The functional difference between such osseous brushes projecting back from the skull and an unossified ligament attaching to the rear of the skull would seem to be slight. With regard to extensions of musculature into or over the skull, it may be that extension of musculature under the lower surface of the cranium appeared earliest. At least, it occurs to a moderate degree in *Amia* and many lower teleosts, apparently reaching the epitome of its development in *Alepocephalus*. However, the extent to which this development can occur is limited amongst other things by the gill arch system; where, as in *Alepocephalus*, there is a large mass of musculature extending in under the skull, the gill arches are necessarily displaced downward and/or laterally, affecting inter alia the gill cover and opercular structure (see Figs. 1, 3A). Muscle encroachment into and over the skull has a longer history which is linked with that of the actinopterygian dermal roof.

In the chondrosteans and holosteans a series of paired dermal bones formed an almost continuous, presumably protective, roof over the head and nape. The bones forming this roof were the nasals, frontals, parietals, extrascapulars, and posttemporals and laterally the dermopterotics (see, e.g., the pholidophoroid *Ichthyokentema*, Griffith and Patterson, 1963, fig. 1). All of these bones were, in addition, canal-bearing ossifications. In the subsequent evolution of fishes the nasals and extrascapulars retained their canal-bearing properties but usually lost their attributes as portions of a continuous, rigid skull roof. The posttemporals have had a more complicated history. They have gradually exchanged their roofing function for that of a movable strut linking and attaching the pectoral girdle to the back of the skull.

An initial step in this direction is seen in *Amia*, where the medial portion of the posttemporal slides in under the extrascapular to form an attachment to the cranium.

Though the medial end of the posttemporal extends nearly to the middorsal line in *Amia* and the lower teleosts, as it did in the lower actinopterygians, it does not form a direct ligamentous attachment between its medial end and the portion of the cranium immediately in front of it. I believe there is a good functional explanation for this. If such an attachment occurred, any backward pull on the pectoral girdle would cause the lateral end of the posttemporal to swing backward around the medial end as a hinge. However, in passing from the head onto the body, the main lateral line canal passes across the lateral portion of the posttemporal bone (Fig. 9, Ll), and any extensive backward swinging of the lateral end of the posttemporal would rip apart the main lateralis system. What occurs even in *Amia* is that the posttemporal develops an axis of rotation nearer to its outer than to its medial end, which results in far less displacement of its lateral portion. This more lateral axis is brought about by the development of a deep fork of the posttemporal which extends down and in from near the lateral border of the posttemporal to an attachment on the intercalar (or exoccipital in *Alepocephalus*) more or less directly below. The upper fork of the posttemporal develops a ligamentous attachment not to that portion of the cranium ahead of it but to the epiotic lateral to it (Fig. 9). These posttemporal attachments continue throughout the main stem of the Teleostei.

The way that the muscular encroachments on the skull of the holosteans and teleosts have developed on the back and roof of the skull seems to be related to fixed points provided by the posttemporal attachment—the epiotic above and the intercalar below. Perhaps the earliest encroachment to develop is the roofed posttemporal fossae of *Amia*, *Ichthyokentema*, and many lower teleosts. These fossae appear to be merely excavations in the back of the skull to increase the surface for muscular attachment. They lie lateral to the epiotic-intercalar area and seem originally to have been roofed primarily by the dermopterotics. (In my opinion it is best to restrict the term posttemporal fossae to the *roofed*, lateral excavations found in such fishes as *Amia*, *Elops*, etc.)

A second pair of excavations is found medial to the posttemporal fossae in the back of the skull of such a fish as *Albula*. These are separated from the posttemporal fossae by a vertical ridge of bone made up of the epiotics above and the intercalars below. They are divided from one another by a median vertical projection comprised primarily by the supraoccipital.

The supraoccipital is a median bone that does not occur in *Amia* or lower actinopterygians. Nevertheless, the median vertical septum must always have been attached to the skull along the midline. In the teleosts, but not, so far as I can determine, in *Amia*, there is a well-developed middorsal band of muscle more or less separate from the epaxial musculature on either side of it. This median muscle is attached forward to the supraoccipital, which, in lower teleosts, extends back into it as a vertical crest. Indeed, in *Chanos* the posterior end of the supraoccipital is splayed out into a vertically aligned brush, presumably to provide a greater surface of attachment for this muscle. It is this vertical supraoccipital crest which divides the two medial fossae on the back of the skull roof of *Albula*.

The subsequent history of the encroachments of musculature on the skull roofs of teleosts can, I think, be understood in terms of the four excavations in the posterior face of such a fish as *Albula*. The musculature of higher teleosts has, as it were, pushed through the roofs of these four fossae and extended forward over the skull. The diminution in area of surface attachment caused by the loss of the roofs of the four fossae has, in the long run, been more than made up in at least many percoids by the development of vertical ridges rising from the skull roof with their lateral attachment surfaces—the supraoccipital crest medially and frontal-parietal crests more laterally. The frontal-parietal crests extend back to over the epiotics, dividing the musculature that extends in over the skull medial to the epiotics from that external to the epiotics.

Even in such a primitive teleost as *Salmo* the roof of the posttemporal fossae is gone and the body musculature extending over the cranium lateral to the epiotics is exposed above. *Salmo* shows, however, no great encroachment by body musculature onto the skull roof medial to the epiotics, though the “shoulders” of the cranium on either side of the cranium are somewhat rounded. Where these medial portions of the body musculature do extend forward onto the cranium there is usually, though not in eels, a concomitant development of a supraoccipital crest extending forward on the cranial roof. When this occurs, the part of the supraoccipital rising above the skull roof serves for the attachment of paired epaxial muscles, not of the median longitudinal muscle.

In light of the above discussion the variations in body musculature attachments and cranial bones in alepocephaloids will be dealt with. The large masses of hypaxial muscle attaching to the floor of the skull in *Alepocephalus rostratus* would seem to reach their extreme development in that fish.

Alepocephaloids show considerable variation in the amount of epaxial musculature extending into or over the upper portion of the skull. In *Alepocephalus rostratus* there are no posttemporal fossae and very little musculature extending over the skull roof. The same is true of *Bathypriion danae*. Both of these forms have, incidentally, very large dermopterotics. In *Bathylaco* (Fig. 6c), the epaxial musculature extends over the skull roof laterally and forward below the dermopterotics, which thus form the roofs of posttemporal fossae. In *Xenodermichthys* (Fig. 6b), this roof is gone, and the dermopterotic is reduced to a relatively small, anterolateral bone.

Certain points about body muscle—cranial bone relationships are brought out by these variations in alepocephaloids. It would seem that when the epaxial musculature extends forwards on the upper portion of the skull, its first extension is into an attachment *below* the dermal covering bones, e.g., to the walls of posttemporal fossae. The attachments of such musculature may be to cartilage or endochondral bone. When the roofs of these fossae are reduced or disappear, the primary effect is a reduction in the extent of dermal roofing elements, e.g., the dermopterotics and parietals in *Xenodermichthys* (Fig. 6b). But even in *Xenodermichthys* the musculature has come to extend to some extent *over* the surface of the dermopterotic. And, of course, in higher teleosts the musculature often extends *over* the parietals and frontals as well.

The gill arches

The gill arch system of *Alepocephalus rostratus* was described in a general way by Gegenbaur (1878). The posterior portion of this system has been discussed by Nelson (1967, pp. 75, 76 and fig. 1b) and the hyoid arch and branchiostegal rays by McAllister (1968, pp. 37, 38).

The hyoid apparatus. In *Alepocephalus rostratus* there are two superficial hypohyal ossifications well separated by cartilage. The upper provides a source of attachment for the ligamentous tissue connecting the hyoid apparatus to the glossohyal and basibranchials, and the lower provides attachment for the ligament to the urohyal. The ceratohyal is considerably narrower in the middle than at either end; it has no foramen and is separated by cartilage from the hypohyals anteriorly and the epihyal posteriorly. The cartilaginous area separating the epi- and ceratohyal is expanded below both bones. The epihyal tapers rather abruptly posteriorly, ending in a cartilaginous nodule which provides a surface for articulation of the interhyal. The interhyal is cartilaginous except for an anterolateral surface ossification to which ligamentous tissue is attached.

There are six, widely spaced branchiostegal rays in *Alepocephalus rostratus*. The anteriormost branchiostegal inserts behind the middle of the ceratohyal. The first two are attached to the base of the ceratohyal medial to the protractor hyoidei muscles (Kirkhoff, 1958) which extend from the symphysis of the mandible back to an insertion on the outside of the ceratohyal slightly behind its middle. The four branchiostegals behind this point are attached to the outer surface of the hyoid arch. The anteriormost of these articulates with the cartilage just below and behind the posteroventral end of the ceratohyal; the posterior three insert on the epihyal. The posterior four branchiostegals are very long and nearly straight, extending back below the subopercle; they are slightly laminar near the base but extend beyond the laminae as long, roundish, flexible struts.

The nature of the branchiostegal rays differs considerably among alepocephaloid fishes. Both the number (4-13) (Marshall, 1966; McAllister, 1968) and the form vary. In alepocephalids the uppermost ray is a long, thin strut which, at least in *Xenodermichthys* (Fig. 3A), seems to form a prop for the lower corner of the opercle. Conversely, in such fishes as *Searsia* (Fig. 3B), the upper branchiostegals are short and lath-like.

The functional gill arches. There are four gill slits. The first three are wide. However the fourth extends up only to about the level of the corner of the arch. From there it extends backward, curving upward, as a closed pocket. This pocket is continuous with the pharynx medially and forms a lateral diverticulum from it on either side. From the front and rear each diverticulum is invaded by large gill rakers that face inward on the front and rear of the diverticulum. The anterior edges of the gill rakers of the back wall intermesh between the posterior edges of the gill rakers of the front wall to more or less completely obliterate the central cavity of each diverticulum. The musculature suggests that the posterior series of gill rakers can be moved in and out of the cavity to form a triturating mechanism.

The internal surface of the mouth in the branchial arch region and elsewhere has

occasional small villi protruding from the surface. There are also well-developed gill rakers on the arches, which seem normal and lath-like, not spiniferous. The only teeth on the gill arch system are the series of small teeth on the pharyngeal bones, all of which have backwardly curved, pointed tips. The teeth on the lower pharyngeals and on the first two upper pharyngeal plates are in single rows; those on the third upper pharyngeal plate are in two or three rows. Of the plates bearing the pharyngeal teeth the lower seem to be completely fused to the underlying endochondral bone, the anterior upper plate is closely united to the bone below, and the posterior two are completely separate. The relationship between the toothless dermal plates and the underlying bone is complex. In the tongue, the dermal component is separate, forming a V-shaped element with the angle of the V posterior. There also appears to be a thin median strut extending forward over the cartilage from the second basibranchial and another extending between basibran-

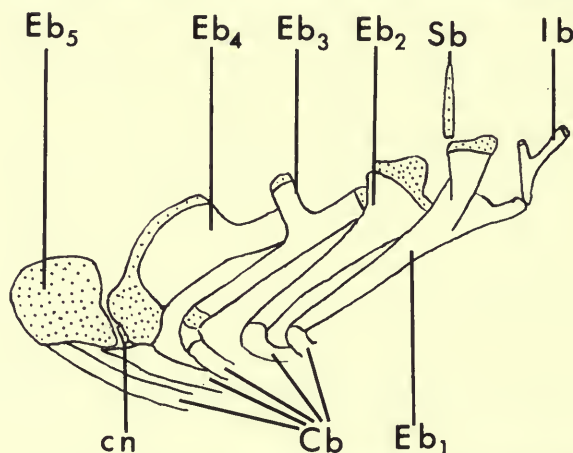


FIG. 10. Upper portion of the gill arches of right side of *Alepocephalus rostratus*, lateral view. Cartilage stippled.

chials two and three, but these seem to be fused to the basibranchials underlying them.

Endochondral ossifications comprise basibranchials 1 through 4, hypobranchials 1 through 3, ceratobranchials 1 through 5, epibranchials 1 through 4, and infrapharyngobranchials 1 through 3. Elements that remain entirely cartilaginous are the suprpharyngobranchial, the large cartilage bordering the epibranchial organ laterally (Fig. 10, Eb5), and basibranchial 5. This last is a very large element, extending as a long strut posteriorly; basibranchial 5 is, indeed, somewhat longer than basibranchials 2, 3, and 4 combined.

What is here considered to be epibranchial 5 (see Fig. 10) is a large squarish plate forming a cap over the lateral end of each pharyngeal diverticulum. A band of musculature (not shown in Fig. 10) extends from its posterior surface to the posterolateral face of ceratobranchial 5. There is also a small, free cartilaginous nodule on the posteroventral surface of each epibranchial 4. It is possible that these nodules and not the plates capping the diverticula represent epibranchial 5.

The upper pharyngeal series of the two sides are widely separated from one another on the midline. The basibranchials form a raised longitudinal ridge.

The same sort of lateral pharyngeal diverticula as those found in *Alepocephalus rostratus* also occur in the alepocephalid *Xenodermichthys socialis*. However, I did not find them in *Searsia koefoedi*.

The axial skeleton

Anterior vertebrae and associated structures. Above the front of the anteriormost vertebra is a separate plate-like bone on either side of the nerve cord which bears a slight, posterodorsally projecting spine (Fig. 11, not shown in Fig. 7B). This is

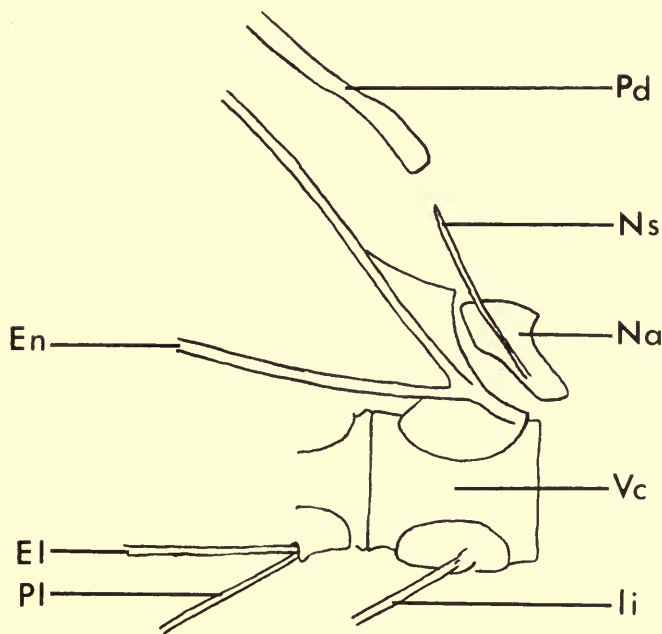


FIG. 11. Anterior vertebrae and associated structures of *Alepocephalus rostratus*, from the right side.

presumably the neural arch and spine of the centrum that has become fused to the skull (see above).

The anteriormost vertebra is not reduced in size. Its centrum appears to be mainly or wholly unossified. Inserted in the centrum are four ossifications, two on either side. A small knob projects from the ventral one. To the posterior surface of this knob is attached a ligament that extends back parallel to the pleural rib of the second vertebra (Fig. 11, li). The dorsal ossification serves as a base for two very long bony but fine projections as well as for a flange that borders the nerve cord. The upper of these projections doubtless represents the neural spine and the lower the epineural intermuscular bone of higher teleosts.

The second vertebra differs from the first in that the ventral projection serves as a

basis for the insertion of two autogenous, backwardly projecting ossifications. Presumably the lower of this pair represents the pleural rib and the upper the epipleural. Above, the same two bony projections occur as on the first vertebra, neither of which is autogenous.

Aside from the centrum, the vertebral structures mentioned up to this point are all paired. However, there is also a long median strut extending up and back from above the first neural spine (Fig. 11, Pd). This strut is very long and somewhat anteroposteriorly expanded. At its dorsal end it forms a roundish flat plate on the surface of the flesh just below the skin. Another difference between this median strut and the projections hitherto mentioned is that it is at least partly cartilaginous; in any event the portion just below the superficial plate shatters easily (as cartilage does).

Posterior abdominal vertebrae. At the level of the last two abdominal vertebrae the following changes have taken place as compared with the anterior vertebrae described above. The pleural rib seems to have become fused to its socket and the epipleural rib articulates with the outside surface of the base of the pleural rib. Above, all trace of a plate-like neural arch element seems to have disappeared, leaving only the neural spine and epineural rib united basally with their presumably osseous nodule.

Caudal vertebrae. In the region below the front of the dorsal fin of *Alepocephalus rostratus* the neural and hemal arches pass directly into median spines. The bases of these elements seem to be fused into the centrum. There are no epipleural or epineural elements with bases on the vertebrae in this area.

Farther back, the hemal arches on pre-ural vertebrae 1 and 2 are autogenous, but those farther forward are not. None of the neural arches ahead of the caudal skeleton is autogenous.

Caudal skeleton and caudal fin. The caudal skeleton of *Alepocephalus rostratus* has been illustrated on two occasions (Gosline, 1960; and Patterson, 1968, also in Nielsen and Larsen, 1968, fig. 10) based on a dried preparation in the British Museum. Though this dried skeleton has been well prepared, certain features can be added from the undried dissection.

There are six hypurals, two below and four above. Hypurals three and four have become completely or almost completely united as Patterson's (1968) figure indicates. The last hemal element and the lower three hypurals have cartilaginous caps by means of which they articulate with the centra. The last hemal element articulates with pre-ural centrum 1 and the second hypural with first ural centrum. The first hypural, which has a well-developed articular head, straddles the area in between. This is not indicated in the dried skeleton, where hypural 1 has a well-developed association with ural 1—see Gosline's or Patterson's illustration. It may be that the two specimens represent individual variations. Or it may be that in drying the base of hypural 1 has shifted backward.

Above the hypurals and below the uroneurals, what is either a sheathed notochord or a cartilaginous replacement of it becomes exposed somewhat ahead of the level of the base of the uppermost hypural. From here it extends back free of the uroneurals into the caudal fin. It terminates at a somewhat weakly developed socket

under the base of the lowermost of the upper unbranched rays at about the level at which the ray becomes segmented, i.e., it underlies the unsegmented basal portion. On the surface of the " notochord " behind the second uroneural there are two small, somewhat nodular concretions, possibly UN₃ of Gosline and UN₃ and 4 of Patterson. However, these concretions differ from the overlapping uroneurals and ray base in being formed in, not outside and separate from, the " notochordal " sheath. (Norden, 1961, p. 709 has described similar nodular formations in the cartilaginous " urostyle " of *Thymallus*.)

There are two pairs of well-developed uroneurals and three epurals. The posterior two epurals are equally long and very roughly parallel. The posterior runs for much of its length between the uroneurals and its anterior portion is not shown by Gosline or Patterson. The anterior epural is small and quite separate. It roughly parallels the posterior neural spine and extends down to just in front of the small neural flange from the first ural vertebra. This flange, which extends between the uroneurals, is median distally but divided proximally, arching over the nerve cord.

I cannot find that the last neural spine or the one previous to it are cartilage-based or autogenous.

In the caudal fin there are 17 branched rays, 9 above and 8 below. The outer principal rays of the caudal fin have ligaments attached to their surfaces part way out along the ray and tapering, more or less pointed bases. The central four rays have expanded, disk-like bases.

On the midline of the caudal peduncle behind the dorsal and anal fin there is a series of flap-like backward extensions that doubtless represent the scale pockets. Sequentially following these is a series of progressively larger accessory rays, 13 above and 15 below. Unlike the dorsal, anal, and principal caudal rays, the anterior accessory rays have no muscle or ligament attachments and no endoskeletal supports. The anterior accessory rays are paired, somewhat tapering, unsegmented, hair-like structures, with the two halves of each element only loosely bound together; only the much heavier, posteriormost accessory rays are segmented.

The pectoral girdle and pectoral fins

The deep arm of the posttemporal very shortly becomes a ligament which passes into what appears to be the posterior rim of the exoccipital. (If there is a separate intercalar I cannot make it out.)

The postcleithrum extends down over, and nearly parallel with the upper portion of the cleithrum (Fig. 12). I can find no indication whatsoever of any postcleithrum. At the upper end of the cleithrum there is a deep notch through which Baudelot's ligament passes from the inside (Fig. 12,bl). From this point Baudelot's ligament passes inward through the hypaxial musculature in close association with one of the intersegmental septa (that between hypaxial myotomes four and five) to an attachment on the side of the first fully developed vertebra.

The uppermost pectoral ray articulates directly with the scapula, or rather with a cartilaginous cap covering the scapular condyle. This condyle is continuous with the rest of the bone and I can see no evidence in the large *Alepocephalus rostratus* of a

separate origin for the scapular condyle. Below the scapular condyle are four actinosts of increasing length. Each of these actinosts consists of bone tipped at either end by cartilage. They do not lie in a single vertical plane basally, though they do distally; rather, the base of the lowermost actinosts extends in to an articulation somewhat medial to that of the one above it.

Except for the two upper and two lower pectoral rays, the inner (but not the outer) halves of the ray bases insert on cartilaginous nodules (which recall the cartilaginous nodules at the base of the rays of the vertical fins, Fig. 14). There are five of these nodules, and the inner halves of the ray bases ride between them so that there is essentially one per ray. However, the uppermost nodule is somewhat larger than the others and extends under two rays. Under the lowermost ray base there is a heavy bed of membranous tissue, but it seems to contain no cartilaginous nodule.

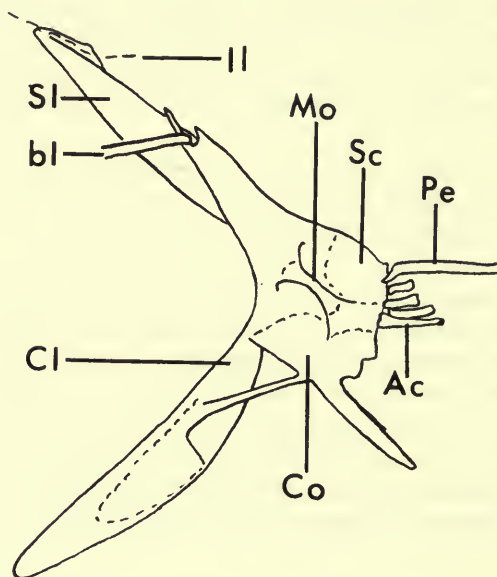


FIG. 12. Internal view of right side of pectoral girdle of *Alepocephalus rostratus*.

There are nine pectoral rays in *A. rostratus*, all segmented and all, except apparently the upper (which is broken), branched. There is no separate splint above the uppermost pectoral ray. However, the base of the uppermost ray is complex and I think it probable that a splint has become fused with its inner "half". Of the two "halves" that make up the uppermost pectoral ray, the outer is similar to the bases of the outer halves of the rays below and takes no part in the articulation with the scapula. The inner half is broadly tipped with cartilage, which forms the articulating surface of the ray.

The pelvic girdle and associated structures

The pelvic girdle consists of a plate of bone with a long forward strut set in cartilage.

There is also a separate cartilaginous nodule underlying the inner fin rays (Fig. 13).

Outside of the outermost fin rays, there is the separate, unarticulated bony strut found in so many lower teleosts (Gosline, 1961). There are seven pelvic rays, all but



FIG. 13. Right half of pelvic girdle of *Alepocephalus rostratus*, from below.

apparently the outermost branched and all segmented. The innermost articulates basally with the pelvic nodule just lateral to its tip, the next two progressively lower down on the lateral rim of the nodule.

The dorsal and anal fins

The anterior two dorsal rays articulate directly with the first pterygiophore (Fig. 14); they have no lateral flanges. The third and fourth (and presumably succeeding)

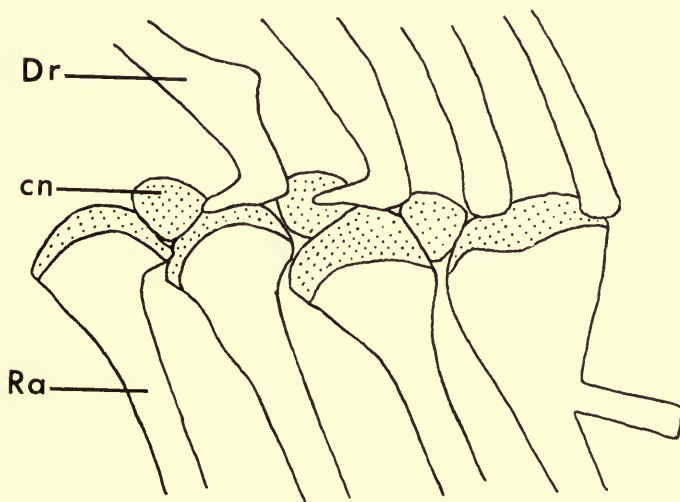


FIG. 14. Anterior dorsal rays and their endoskeletal supports in *Alepocephalus rostratus*, from right side. Cartilage stippled.

rays are each inserted between and articulate primarily with nodules of cartilage which in turn interdigitate between the distal heads of the main pterygiophore. The

resemblance between the dorsal and pectoral ray articulations in *Alepocephalus rostratus* has already been noted.

The last two dorsal rays are split to the base. The last two rays articulate directly with a single expanded pterygiophore. The ray before the last two articulates with a cartilaginous nodule.

The dorsal pterygiophores are mostly enclosed in the fleshy lobe and do not extend much deeper into the body than the base of this lobe. The well-developed fleshy lobes at the base of the dorsal and anal fins (Fig. 1) are made up entirely of the musculature to the individual fin rays. The fin rays themselves are all directed backward, the longer posterior rays more so than the anterior. The structure of the dorsal and anal fins suggests to me that *Alepocephalus* may use these fins as a major source of normal forward locomotion.

VISCERAL ORGANS

The peritoneum of *Alepocephalus rostratus* is black. The liver has a single large lobe on the left side with a knob projecting to the right which may represent the right lobe. The large, heavy-walled oesophagus leads into a U-shaped stomach. At the pyloric end of the stomach are 18 finger-like caeca.

The bulbus arteriosus of the heart is rather expanded and thin-walled. I can find no valves within it.

I did not find the gonads in the specimen of *Alepocephalus rostratus*, but Marshall (1966) has described and figured an ovary and oviduct in *Bathypriion danae*.

LIFE HISTORY

Beebe (1933, pp. 21-56, figs. 2-15) gives an extensive account of the juvenile stages of the searsid genus *Bathytroctes* based on 89 specimens 9.5 to 56 mm. long. These small individuals were essentially like the adults; i.e., development is direct and there is no specialized larval form. Beebe's specimens were taken in the depth range at which adults occur (500 to 1000 fathoms) suggesting no vertical migration during ontogeny. His figure of a 9.5 mm. individual (Beebe, 1933, fig. 8A) shows a yolk sac extending for a third of the length of the fish, indicating a very large egg. In this regard, Nielsen and Larsen (1968, pp. 228-229) report eggs in the female of *Bathylaco nigricans* up to 2.7 mm. in length. They suggest that *B. nigricans* is an oviparous, non-hermaphroditic species.

SUMMARY OF SALIENT CHARACTERS OF ALEPOCEPHALOID FISHES

Before attempting to assess the systematic position of the alepocephaloid fishes it may be well to summarize what would seem to be the salient characters of the group so far as known.

1. No ethmoidal commissure.
2. Supraorbital canal not joining the infraorbital canal.
3. Two free extrascapulars on each side, the supratemporal commissure incomplete.
4. Lateral line in the posttemporal region borne by a separate ossicle, not by the posttemporal itself.

5. Maxillary included in the gape.
6. Two supramaxillaries.
7. Dermopalatine and autopalatine separate.
8. A basipterygoid process may be present.
9. A single large, apparently dermal ethmoid ossification.
10. Supraoccipital separating the parietals.
11. Musculature for adducting the suspensorium inserting well forward, on the parasphenoid.
12. No subtemporal fossae.
13. A large block of hypaxial musculature attached to the floor of the skull on either side posteriorly.
14. A vertebral centrum fused into the base of the skull posteriorly.
15. A well-developed, cartilaginous suprapharyngobranchial on the first gill arch.
16. Triturating organs formed by the last two gill arches in lateral diverticula of the pharynx in some.
17. Neural spine and epineural elements arising from a common osseous base.
18. Pleural and epipleural ribs from the second complete vertebra.
19. Caudal skeleton with the anterior uroneural extending forward onto the second preural centrum.
20. Pectoral actinosts bordered externally by five cartilaginous nodules which are essentially interradiar.
21. Mesocoracoid present.
22. Pelvic girdle with a single cartilaginous nodule, with which the three innermost pelvic rays articulate.
23. Dorsal fin inserted well back on the body.
24. No adipose fin.
25. No swim bladder.
26. A relatively large egg; no specialized larval form.
27. No vertical migration during ontogeny.

THE RELATIONSHIPS AND A PROVISIONAL DEFINITION OF THE ALEPOCEPHALOID FISHES

Characters that would seem to represent portions of a common teleostean heritage are retained here and there among various living groups. A relatively high number of such characters occurs among alepocephaloids, e.g., the absence of a junction between supraorbital and infraorbital lateralis canals, the maxillary included in the gape and with two supramaxillaries, the separation between autopalatine and dermopalatine and between autopterotic and dermopterotic, the basipterygoid process, the suprapharyngobranchial element, the epibranchial organ, the neural spine and epineural bone arising from the same basal plate, the anterior uroneural of the caudal skeleton extending forward on to the second pre-ural centrum, the mesocoracoid arch, and the cartilaginous nodule at the base of the inner pelvic rays.

These characters show clearly that the alepocephaloids belong among the basal groups of living teleosts. However, they do not indicate which of the other basal

groups the alepocephaloids are most closely related to. In the first place, these presumably ancestral alepocephaloid traits are distributed among other lower teleosts in a rather haphazard manner. The basipterygoid process is found elsewhere today only among the osteoglossoid fishes; other such features occur elsewhere among elopoids, clupeoids, gonorhynchoids, or/and salmonoids, etc. In any event Ridewood (1904), Hennig (1966), and a host of others have pointed out that relationships cannot satisfactorily be determined on the basis of ancestral characters. Such features, which two or more groups happen to have retained, can at best suggest ways in which these forms have not evolved.

As to ways in which the alepocephaloids have evolved, these seem to be few. The alepocephaloids appear to represent an old, generalized teleostean stock that has taken up an oceanic, midwater existence, and such specializations as they do have appear to be adaptations for that existence.

Thus the alepocephaloids may possess bioluminescent organs of various types, the most notable of which is the shoulder organ of the Searsidae (Parr, 1951, 1960). Neither this, which appears to be unique among fishes, nor the various other light organs more rarely represented among alepocephaloids (Parr, 1960), seems to provide clues concerning relationships.

Alepocephaloids have no swimbladder. However, this structure has been repeatedly lost in midwater fishes (Denton & Marshall, 1958). Again, little indication of relationship is provided. Probably the most that can be said is that groups without swimbladders are not usually closely related to forms that have gone to the trouble of developing these structures into specialized sound amplifiers.

Denton & Marshall (1958) have concluded that alepocephaloid structure is such as to preclude strong, continuous swimming, but that those fishes may effectively dart short distances. For a mode of life of this sort abrupt acceleration from a standing start is advantageous. This would seem to be facilitated by a concentration of vertical fins at the rear of the body. Such a fin configuration and, presumably, mode of life have been adopted by fishes in various environments, e.g., *Esox*, *Sphyræna*, but seem to be particularly common among bathypelagic forms, where, as in alepocephaloids, the dorsal fin is often far back on the body. Thus, the posteriorly placed dorsal fin of alepocephaloids is not unique or diagnostic. However, it seems to provide as good a starting point as any for a discussion of alepocephaloid relationships.

Aleev (1963) has pointed out that the dorsal fin may play one or more of four possible roles: (1) it may provide a keel to prevent sideslipping when a fish is making a turn; (2) it may serve to stabilize forward trajectory (as the feathers on an arrow do); (3) it may act as a rudder to aid in steering; and/or (4) it may aid in forward propulsion. The keel function seems to differ from the other three in several respects. In the first place, the tendency to overshoot a turn depends on forward momentum, which increases with size and forward speed of the fish. Small or slowly moving fishes would seem to have little need for keels. But if a keel is needed, the most effective place for it is over (or under) the centre of gravity. On the other hand, with certain exceptions rudders become more effective with increasing distance from the centre of gravity, and stabilizers and locomotor organs if placed posteriorly

(Aleev, 1963). On the basis of these considerations it would seem probable that the more or less medially placed dorsal fins of such lower teleosts as *Elops*, *Chanos*, and *Salmo* serve primarily as keels.

With regard to these three genera, the first question that arises is whether the forward position of the dorsal fin is not a specialization among relatively large, active fishes? Is it possible that this is one of the features made advantageous in some, perhaps all, of the early Teleostei by the reduction in scaly armour, the perfection of the externally symmetrical caudal fin (Patterson, 1968), etc.?

Second, if a median keel is advantageous only in relatively large, powerfully swimming fishes, then what do the small, weakly swimming larval and juvenile stages of these same fishes do with their dorsal fins? Two rather different answers to this question have been provided by *Elops* and *Salmo*.

Elops has a long, transparent, ribbon-like "leptocephalous" larva, which undoubtedly swims by undulation of the body. In this larva the dorsal and anal fins are placed far back, just ahead of the tail. As the larval form grows and transforms into the adult, the dorsal (and anal) fins move forward on the body. If the forward dorsal position of the adult *Elops* is a specialization, the extreme posterior position of the dorsal in the larva would also seem to be a specialization, but in the opposite direction. Presumably the change in position is related to the different methods and requirements of swimming in the young and adult *Elops*. In *Chanos* and the clupeoids (see, for example, Delsman, 1926, and François, 1956), forward movement of the dorsal fin during ontogeny also occurs, but to a lesser extent than in *Elops*.

Salmo lays large eggs, and the juveniles that hatch out have essentially the adult form. The dorsal fin first appears in about its adult, forward position. However, *Salmo* does have, behind the dorsal fin, a rayless adipose fin of problematic function (Wassnetzov, 1935; Kosswig, 1965). Two questions come to mind. One is whether the adipose fin of *Salmo* does not play the same role, whatever that is, of the more posteriorly placed dorsal fin of the juvenile herring, *Chanos*, etc.? Second, could the adipose fin serve in some minor way to offset the otherwise asymmetrically placed anal fin below it? The anal fin, acting as a rudder, might have two effects worth offsetting. One is to twist the posterior end of the body and the other is to lift it.

Though they only bear peripherally on the alepocephaloid condition, a number of different groups have developed forms with a long anal fin which is presumably the principal locomotor organ, a tapering body, and a dorsal fin which, if present, is well forward. Fishes of this type are the Gymnarchidae, *Coilia* among the Engraulidae, the Halosauridae, and certain catfishes. Among these, the adipose fin tends to be lost among the catfishes, and the dorsal fin to be far forward in the larval halosaur (Mead, 1965).

Among alepocephaloids, *Bathylaco* is known to lay large eggs (Nielsen & Larsen, 1968) and *Bathytroctes* develops without any peculiar larval form or anterior movement of the dorsal fin with growth (Beebe, 1933). This development would seem to be quite unlike that of elopoids, clupeoids and *Chanos*. Further differentiation between alepocephaloids and *Elops* or clupeoids is the absence of a subtemporal fossa and any swimbladder to ear connection in alepocephaloids.

The possibility of a relationship between alepocephaloids and *Albula* seems no

greater, partly because of the larval specializations of *Albula* and its presumed derivatives, the eels and halosaurs, but also because of the lateral line peculiarities in the snout of these fishes (Allis, 1903; Gosline, 1961), etc.

Alepocephaloids have the dorsal fin well back on the body and no adipose fin. Other marine teleosts with this fin construction are *Gonorhynchus* and some stomiatoids. I can find no information on the ontogenetic development of *Gonorhynchus*, but it, along with other gonorhynchoids including *Chanos*, has a small mouth with peculiar jaw construction, a reduced number of branchiostegal rays, and one or more cephalic ribs (Greenwood, et al., 1966 : 375). Alepocephaloids show none of these specializations.

Those stomiatoid fishes with a posterior dorsal and no adipose form a highly specialized series of derivatives from forms with an adipose fin and the rayed dorsal farther forward. Though there would seem to be no direct relationship between alepocephaloids and stomiatoids (Weitzman, 1967a, b), the question could perhaps be raised of whether the stomiatoids and alepocephaloids are not two partially parallel endpoints in evolution from a single, if distant, stock. Weitzman (1967a) traces the stomiatoids back to an origin among a group of fishes rather like the present day osmerids. But neither the osmerids nor any of their present day relatives are sufficiently generalized, i.e., "primitive", to have given rise to the alepocephaloids. None of them, for example, have the basipterygoid process or epibranchial organ found among alepocephaloids.

By a process of elimination, then, it appears that the alepocephaloids are perhaps least unlike the osmeroids among modern fishes. Characters held in common by the two groups are much too general in nature to more than suggest the possibility of such a relationship (Ridewood, 1904; Hennig, 1966). They include such features as the absence of forward movement of the dorsal fin during ontogeny, the absence of subtemporal fossae, and the presence of a single elongate uroneural (there are other shorter ones posteriorly) extending forward over the second pre-ural centrum in at least *Alepocephalus*, *Bathylaco* and salmonids. Some osmeroid derivatives have taken up a midwater oceanic existence alongside the alepocephaloids, and among these are forms which have adapted themselves to such an existence in certain alepocephaloid-like ways. This may indicate parallel development from a single basal stock and hence relationships of a distant sort; or, of course, it may be the result of convergent evolution from quite different basal stocks.

Defining the alepocephaloids is hardly less difficult than determining their relationships. Internal characters cannot be used because they are known in at best a few forms among a diverse group. Two skeletal features may be noted as holding promise in future definitions of the group. One is the long anterior uroneural in the caudal skeleton which occurs in *Alepocephalus* and *Bathylaco*. The other is the opercular series of bones. This series, though quite diverse in the species for which it is known (see, for example, Fig. 3) may prove to be peculiar in one way or another throughout the group. Meanwhile, the best that can apparently be done is to define the alepocephaloids in terms of general characteristics which in combination will serve to exclude other groups:

Oceanic, midwater, dark-coloured fishes with the maxillary included in the gape

and the dorsal fin over the posterior half of the body; without a swimbladder, adipose fin, enlarged fang-like teeth, or two long regular rows of small light organs along the lower sides.

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THE GENUS *KELLERIA*
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INTERTIDAL BURROWS IN
MADAGASCAR

A. G. HUMES
and
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Pp. 219-229 : 8 Plates

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CYCLOPOID COPEPODS OF THE GENUS *KELLERIA* (LICHOMOLGIDAE) FROM INTER- TIDAL BURROWS IN MADAGASCAR

By A. G. HUMES & JU-SHEY HO

AMONG the copepods collected by the first author in 1960 and 1963-64 from intertidal burrows in the region of Nosy Bé, in north-western Madagascar, there are (in addition to the seven species of *Hemicyclops* described by Humes, 1965) two species of the genus *Kelleria*, *K. regalis* Gurney, 1927, and *K. pectinata* (A. Scott, 1909). Since the descriptions of both of these species are incomplete, with only the female of *K. pectinata* previously known, the two species are redescribed, including a description of the male of *K. pectinata*.

The copepods were obtained from water pumped from the burrows by means of a small hand-operated bilge pump. *Kelleria* was found only once in burrows whose occupant was known, namely, *K. pectinata* in burrows of the shrimp *Axius* (*Neaxius*) *acanthus* A. Milne Edwards. Although the occupants of other larger burrows (extending down more than a metre) were never seen or collected, it is possible that they were stomatopods.

The field work in 1960 was supported by the Academy of Natural Sciences of Philadelphia, and that in 1963-64 by the U.S. Program in Biology of the International Indian Ocean Expedition. The staff of the Centre ORSTOM de Nosy Bé generously provided certain facilities during the field work.

The study of the material has been aided by a grant (GB-5838) from the National Science Foundation of the United States.

We wish to thank Dr. J. P. Harding for making available to us syntypes of *Kelleria regalis* from the collection of the British Museum (Natural History).

All figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn. The measurements have been made from specimens in lactic acid. The length of the body does not include the setae on the caudal rami. The lengths of the segments of the first antenna have been taken along their posterior non-setiferous margins.

Family **LICHOMOLGIDAE** Kossmann, 1877

Genus ***KELLERIA*** Gurney, 1927

Kelleria regalis Gurney, 1927

(Figs. 1-30.)

MATERIAL COLLECTED. 24 ♀♀, 22 ♂♂, and 16 copepodids in water pumped from

20 large burrows (diameter 3.5 cm.) in muddy intertidal sand, Ambanoro, Nosy Bé, Madagascar, February 15, 1964 [these adults deposited in the British Museum (Natural History)] ; 5 ♀♀, 1 ♂, and 1 copepodid from 5 smaller burrows (diameter 1.5 cm.) in the same locality, February 15, 1964 ; 11 ♀♀, 5 ♂♂, and 5 copepodids from large burrows in muddy intertidal sand, Ampassipohe, Nosy Bé, May 11, 1964; and 1 ♂ from 20 large burrows in intertidal sand, Boloboxo, Nosy Faly, east of Nosy Bé, May 13, 1964.

Female. The body (fig. 1) has a moderately slender prosome, a little thickened dorsoventrally, and a slender elongated urosome. The length is 1.32 mm. (1.25–1.37 mm.) and the greatest width 0.44 mm. (0.42–0.45 mm.), based on 10 specimens. The sclerotization of the body wall is weak. The segment of leg 1 is separated from the head by a dorsal transverse furrow. The ratio of the length to the width of the prosome is 1.55 : 1.

The segment of leg 5 (fig. 2) is $65 \times 153 \mu\text{m}$. Between this segment and the genital segment there is no ventral intersegmental sclerite. The genital segment is elongated (203 μm long), in dorsal view somewhat expanded in its anterior two-fifths (greatest width here 143 μm) and narrower with nearly parallel sides in its posterior three-fifths (width about 104 μm). The areas of attachment of the egg sacs are located laterally on the anterior expanded portion of the segment. Each area (figs. 3 and 4) bears a small naked seta 9 μm long, a spiniform process 8 μm , and a little posteriorly removed from these and situated on a noticeable expansion a much longer prominent finely barbed seta 52 μm . The three postgenital segments are $88 \times 91 \mu\text{m}$, $65 \times 83 \mu\text{m}$, and $52 \times 78 \mu\text{m}$ from anterior to posterior. The anal segment has a row of minute spinules posteriorly along the dorsolateral and ventrolateral margins.

The caudal ramus (fig. 5) is moderately elongated, $77 \times 34 \mu\text{m}$ in greatest dimensions including the terminal flange, or 2.27 times longer than wide. The outer lateral seta is 70 μm long and naked. The other setae have lateral spinules. The dorsal pedicellate seta is 65 μm , the outermost terminal seta 81 μm , the innermost terminal seta 109 μm , and the two median terminal setae 220 μm (outer) and 330 μm (inner), both inserted dorsally to a small terminal flange bearing a marginal row of minute spinules.

The dorsal surface of the prosome and urosome bears a few small hairs (sensilla) and refractile points; the ventral surface of the urosome almost entirely lacks ornamentation. The ratio of the length of the prosome to that of the urosome is 1.22 : 1.

The egg sacs (fig. 1) are oval and reach as far as the second postgenital segment. Each sac is about $308 \times 165 \mu\text{m}$ and contains a moderately small number of eggs about 62 μm in diameter.

The rostrum (fig. 6) is well-defined, with a rounded posteroventral margin, and projects slightly in lateral view (fig. 7).

The first antenna (fig. 6) is about 300 μm long. The lengths of the seven segments are : 22 (55 μm along its anterior margin), 73, 18, 44, 40, 44, and 28 μm respectively. The armature is : 4, 13 (5+8), 6, 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. All the setae are naked.

The second antenna (fig. 8) is slender. The fourth segment is elongated, 86 μm

along its outer edge to the seta, 73 μm along its inner edge, and 19 μm wide, and bears terminally two claw-like jointed setae and five slender simple setae. The outer margins of the second and fourth segments bear rows of small spinules.

The labrum (fig. 9) has two broad hyaline posteroventral lobes. Immediately in front of the labrum the ventral surface of the head is slightly protruded as in figure 7.

The mandible (fig. 10) has on its convex edge a cluster of slender spinules followed by a series of large teeth (the second one smaller than the immediately succeeding teeth), and on its concave edge a row of stout spines. The terminal flagellum is moderately long and barbed. The paragnath (fig. 11) bears very slender spinules. The first maxilla (fig. 12) bears three barbed setae and a subterminal weakly articulated seta ornamented with a terminal tuft of minute spinules. The second maxilla (fig. 13) has a large basal segment which bears distally a small sharp spiniform process. The second segment bears a minute ventral spinule, a posterior surficial naked seta, and a large strongly barbed spine; the short spiniform lash bears three large spines (the middle one shorter than the other two) followed by several smaller spines. (In the right second maxilla of one female an abnormal spination occurred as shown in fig. 14.) The maxilliped (fig. 15) shows a proximally directed acutely pointed fringed process on the inner margin of the first segment. Both of the two setae on the second segment have a strong spinule on their proximal margins in addition to smaller spinules. The small third segment bears four elements.

The area between the maxillipeds and the first pair of legs is slightly protuberant.

Legs 1-4 (figs. 16, 17, 18, and 19) have the following armature (the Roman numerals indicating spines, the Arabic numerals representing setae) :

P ₁	coxa	0-1	basis	1-0	exp	I-0	I-1	III, I, 4
					enp	0-1	0-1	I, 5
P ₂	coxa	0-1	basis	1-0	exp	I-0	I-1	III, I, 5
					enp	0-1	0-2	I, II, 3
P ₃	coxa	0-1	basis	1-0	exp	I-0	I-1	III, I, 5
					enp	0-1	0-2	I, II, 2
P ₄	coxa	0-1	basis	1-0	exp	I-0	I-1	II, I, 5
					enp		II, I	

The inner seta on the coxa of legs 1-3 is long and plumose, but in leg 4 this seta is shorter (25 μm) and finely barbed. The inner margin of the basis of all four legs bears a row of hairs. The 1-segmented endopod of leg 4 (fig. 19) is 75 μm long, including the distal spiniform processes; the part of the segment proximal to the outer marginal notch is expanded (25 μm wide) with long hairs along its outer margin; the distal part is narrower (21 μm wide) with very small outer spinules. The inner plumose seta is 47 μm , and the two terminal fringed spines are 40 μm (outer) and 68 μm (inner).

Leg 5 (fig. 20) has a free segment about 120 $\times$ 53 μm in greatest dimensions with a distally directed tooth-like spinous process about 19 μm long on the inner margin. The two terminal spiniform elements are 65 μm (outer) and 67 μm (inner) in length and unilaterally fringed. The seta on the body near the free segment is 60 μm and feathered. An abnormal left free segment is shown in figure 21 (the segment of the right fifth leg in this female having a normal form).

Leg 6 is probably represented by the two setae near the attachment of each egg sac (fig. 4).

The colour in life in transmitted light is slightly amber, with indistinct red lines ventrally around the epimera of the metasomal segments ; a few orange-red globules in the prosome ; the eye dark red ; the egg sacs grey to reddish orange.

Male. The body (fig. 22) resembles in general form that of the female, though the prosome is less pointed anteriorly. The length is 1.05 mm. (1.00–1.09 mm.) and the greatest width 0.32 mm. (0.31–0.34 mm.), based on 10 specimens. The ratio of the length to the width of the prosome is 1.70 : 1.

The segment of leg 5 (fig. 23) is $46 \times 91 \mu\text{m}$. The genital segment is $156 \times 130 \mu\text{m}$, with only slightly rounded lateral margins in dorsal view. The four postgenital segments are $62 \times 62 \mu\text{m}$, $62 \times 58 \mu\text{m}$, $43 \times 53 \mu\text{m}$, and $46 \times 60 \mu\text{m}$ from anterior to posterior.

The caudal ramus is similar to that of the female.

The surface of the body bears very few hairs and refractile points. The ratio of the length of the prosome to that of the urosome is 1.26 : 1.

The rostrum is like that of the female.

The first antenna resembles that of the female but three long aesthetes are added, two on segment 2 and one on segment 3. The second antenna, labrum, mandible, paragnath, and first maxilla are similar to those in the female.

The second maxilla (fig. 24) has an arrangement of spines on the spiniform lash different from that in the female, with two short spines between each of the three large spines.

The maxilliped (fig. 25) is slender and 4-segmented, assuming that the proximal part of the claw represents a fourth segment. The second segment bears inwardly two setae, one of them sickle-shaped with a hyaline concave margin, and three rows of spinules. The claw is $234 \mu\text{m}$ along its axis and carries proximally two very unequal setae.

The area between the maxillipeds and the first pair of legs is only slightly protuberant.

The formula for the armature of legs 1–4 is like that of the female, except for the last segment of the endopod of leg 1 (fig. 26) which is I, I, 4. This endopod is strongly geniculate between segments 2 and 3. The lateral spinules on the inner of the two spines on the third segment are peculiarly broad and obtuse. The last segment of the endopod of leg 2 (fig. 27) also shows sexual dimorphism, the outer of the two terminal spines being naked and the anterior surface of the segment near the insertion of this spine having an erect sharply pointed recurved spiniform process. Legs 3 and 4 are like those of the female.

Leg 5 (fig. 28) has a small unornamented free segment $26 \times 12 \mu\text{m}$, without an inner spinous process. The two terminal elements comprise an outer naked seta $37 \mu\text{m}$ long and an inner spiniform barbed spine $31 \mu\text{m}$.

Leg 6 (fig. 29) consists of a posteroventral flap on the genital segment bearing two setae, one $50 \mu\text{m}$ long and feathered, the other $39 \mu\text{m}$ and naked, and a sharp spiniform process.

The spermatophore (fig. 30), attached to the female in pairs, is elongated, $120 \times 60 \mu\text{m}$, not including the neck.

The colour in life resembles that of the female.

DISCUSSION. Gurney's description of *Kelleria regalis* from the Suez Canal shows many similarities with our Madagascan material. For the purpose of a more detailed comparison we have examined by dissection two syntypes of this species, a male and a female, Brit. Mus. (Nat. Hist.) 1928.4.2.21.

Our specimens agree in all major respects with the syntypes. There are, however, four rather minor differences. The body size of the syntypes is a little larger (the female 1.45×0.53 mm., the male 1.32×0.46 mm.). The caudal ramus is relatively a little longer, in the female $99 \times 39 \mu\text{m}$ with the ratio $2.5 : 1$, and in the male $104 \times 34 \mu\text{m}$ with the ratio $3.0 : 1$. On the convex edge of the mandible there are two small teeth immediately following the large tooth, instead of only one small tooth as in the Madagascan specimens. On leg 5 of the female the two terminal setae are more unequal in length, the outer being $60 \mu\text{m}$, the inner $92 \mu\text{m}$. Since the other features of the syntypes are identical with those in our specimens, we conclude that the Madagascan material represents *K. regalis*, and that such minor differences as those observed in the two syntypes studied represent intraspecific variation.

We are unable to evaluate conclusively the specific merit of *Kelleria rubimaculata* Krishnaswamy, 1952. Like Stock (1967) we have not found in Krishnaswamy's description dependable differences between this Indian species and *K. regalis*, except the shorter body length (the female of *K. rubimaculata* being 0.7 mm. long and the male 0.637 mm.).

Kelleria pectinata (A. Scott, 1909)

(Figs. 31-53.)

MATERIAL COLLECTED. 8 ♀♀, 1 ♂, and 4 copepodids in water pumped from 20 large burrows (diameter 3.5 cm.) in muddy intertidal sand, Ambanoro, Nosy Bé, Madagascar, February 15, 1964 [of these 6 ♀♀ and 1 ♂ deposited in the British Museum (Natural History)]; 6 ♀♀, 1 ♂, and 3 copepodids from 5 smaller burrows (diameter 1.5 cm) in the same locality, February 15, 1964; 1 ♀ from large burrows in muddy intertidal sand, Ampassipohe, Nosy Bé, May 11, 1964; 1 ♀ from large burrows in clean intertidal sand, Nosy Roty, east of the northern end of Nosy Sakatia, near Nosy Bé, May 12, 1964; 8 ♀♀ from 20 large burrows in intertidal sand, Boloboxo, Nosy Faly, east of Nosy Bé, May 13, 1964; and 1 ♀ from burrows of the thalassinidean shrimp *Axius* (*Neaxius*) *acanthus* A. Milne Edwards, Andilana, Nosy Bé, Oct. 8, 1960.

Female. The body (fig. 31) resembles in general form that of *K. regalis*, but the prosome is less pointed anteriorly. The length is 1.01 mm. (0.96-1.09 mm.) and the greatest width is 0.37 mm. (0.34-0.39 mm.), based on 8 specimens. The sclerotization of the body wall is weak and the segment of leg 1 is separated from the head as in *K. regalis*. The ratio of the length to the width of the prosome is $1.63 : 1$.

The segment of leg 5 (fig. 32) is $60 \times 109 \mu\text{m}$. Between this segment and the genital segment there is no ventral intersegmental sclerite. The genital segment, $156 \mu\text{m}$ long, shows in dorsal view two lateral protrusions anteriorly, where the width is $127 \mu\text{m}$. The areas of attachment of the egg sacs are situated laterally in the anterior

third of the segment. Each area (fig. 33) bears a small naked seta $6\text{ }\mu\text{m}$ long, a spiniform process $7\text{ }\mu\text{m}$, and posteriorly and laterally to these a prominent finely barbed seta $45\text{ }\mu\text{m}$. The surface of the segment dorsal to the insertion of this long seta is delicately corrugated. The three postgenital segments are $56\times 63\text{ }\mu\text{m}$, $42\times 60\text{ }\mu\text{m}$, and $50\times 62\text{ }\mu\text{m}$ from anterior to posterior. The posterior margin of the anal segment is smooth.

The caudal ramus (fig. 34) is elongated, $79\times 26\text{ }\mu\text{m}$ in greatest dimensions including the terminal flaps, or 3.04 times longer than wide. The outer lateral seta is $58\text{ }\mu\text{m}$ and the dorsal pedicellate seta $25\text{ }\mu\text{m}$, both naked. The four terminal setae have lateral spinules; the outermost is $108\text{ }\mu\text{m}$, the innermost $117\text{ }\mu\text{m}$, and the two median setae $187\text{ }\mu\text{m}$ (outer) and $234\text{ }\mu\text{m}$ (inner), both inserted between smooth dorsal and ventral flaps.

The dorsal surface of the prosome and urosome has a few small hairs (sensilla) and refractile points; such ornamentation is almost wholly lacking on the ventral surface of the urosome. The ratio of the length of the prosome to that of the urosome is 1.45 : 1.

The egg sacs (fig. 31) are oval and extend a little beyond the caudal rami. Each sac is about $385\times 200\text{ }\mu\text{m}$, and contains a greater number of eggs than in *K. regalis*, with each egg approximately $51\text{ }\mu\text{m}$ in diameter.

The rostrum resembles that of *K. regalis*.

The first antenna is segmented and armed as in *K. regalis*, but the lengths of the segments are slightly different : 21 ($50\text{ }\mu\text{m}$ along its anterior margin), 69, 15, 27, 33, 28, and $33\text{ }\mu\text{m}$ respectively. All the setae are naked.

The second antenna (fig. 35) resembles that of *K. regalis*, but the second and fourth segments are relatively shorter. The fourth segment is $64\text{ }\mu\text{m}$ along its outer edge to the seta, $44\text{ }\mu\text{m}$ along its inner edge, and $17\text{ }\mu\text{m}$ wide. Terminally it bears two claw-like jointed setae (both with their concave margins finely barbed) and five slender simple setae.

The labrum is like that of *K. regalis*. The ventral area of the head immediately in front of the labrum is less protruded than in *K. regalis*.

The mandible (fig. 36) is much like that in *K. regalis*, but the spinules on the convex edge are stouter and arranged in a row rather than a cluster, and the second large tooth in the series distal to these spinules is not unusually shortened. The proximal inner margin of the flagellum is slightly swollen, where the series of teeth merges with the flagellar spinules, as indicated in A. Scott's Pl. LXVIII, fig. 24. Paragnaths were not seen in the dissections made, though probably they are present, since they occur in the male (see fig. 47). The first maxilla (fig. 37) has the same number of elements as in *K. regalis*, but the subterminal element is naked and shows no articulation with the appendage. The second maxilla (fig. 38) resembles that of *K. regalis*, but the spines on the short spiniform lash are differently formed. The maxilliped (fig. 39) has the same number of elements as in *K. regalis*, but on the last segment one spine and the two setae are very short, while the other spine is long and claw-like, as A. Scott showed in his Pl. LXVIII, fig. 26.

The area between the maxilliped and the first pair of legs is slightly protuberant.

Legs 1-4 are segmented as in *K. regalis* and have the same spine and setal formula

as in that species. The exopods of these legs closely resemble those of *K. regalis*, but the endopods differ in certain details. The last segment of the endopod of leg 1 (fig. 40) and its spine are relatively longer. The same is true for the endopod of leg 2 (fig. 41). The last segment of the endopod of leg 3 (fig. 42) is relatively longer and its inner terminal spine is markedly longer in relation to the other two spines than in *K. regalis*. In leg 4 (fig. 43) the inner seta on the coxa is short ($15\text{ }\mu\text{m}$) and naked. The inner margin of the basis is naked. The endopod is $61\text{ }\mu\text{m}$ long, including the distal spiniform processes; the width proximal to the outer marginal notch is $18\text{ }\mu\text{m}$, and distal to the notch $14\text{ }\mu\text{m}$. The inner plumose seta is $36\text{ }\mu\text{m}$, and the two terminal fringed spines are $33\text{ }\mu\text{m}$ (outer) and $53\text{ }\mu\text{m}$ (inner).

Leg 5 (fig. 44) has a slender elongated unornamented free segment, with a slight inner proximal expansion. The length is $67\text{ }\mu\text{m}$, the width at the expansion $19\text{ }\mu\text{m}$, and the width distally $12\text{ }\mu\text{m}$. The outer terminal element is setiform and naked, $33\text{ }\mu\text{m}$, the inner is spiniform and fringed, $50\text{ }\mu\text{m}$. The seta on the body near the free segment is $36\text{ }\mu\text{m}$ and lightly feathered.

Leg 6 is probably represented by the two setae near the attachment of each egg sac (fig. 33).

The colour in life in transmitted light resembles that of *K. regalis*.

Male. The body (fig. 45) is similar in general form to that of *K. regalis*. The length and the greatest width of 2 specimens are $0.78 \times 0.25\text{ mm}$. and $0.80 \times 0.24\text{ mm}$. The ratio of the length to the width of the prosome is $1.80 : 1$.

The segment of leg 5 (fig. 46) is $34 \times 75\text{ }\mu\text{m}$. The genital segment is $121 \times 120\text{ }\mu\text{m}$. The four postgenital segments are $43 \times 52\text{ }\mu\text{m}$, $39 \times 47\text{ }\mu\text{m}$, $29 \times 43\text{ }\mu\text{m}$, and $40 \times 47\text{ }\mu\text{m}$ from anterior to posterior.

The caudal ramus is like that of the female.

The first antenna is similar to that of the female, but has three aesthetes added as in *K. regalis*. The second antenna, labrum, and mandible are like those in the female. The paragnath (fig. 47) is a small lobe with a few hairs. The first maxilla resembles that of the female. The second maxilla (fig. 48) differs from that of the female in the lengths of the spines on the short lash and in the spinulation of the large inner spine. The maxilliped (fig. 49) has four rows of spinules on the second segment. One of the two setae on this segment is recurved, with a short fringe on its convex margin. There are two small knobs near the smaller of the two setae on the proximal part of the claw. The claw is $146\text{ }\mu\text{m}$ along its axis.

The area between the maxillipeds and the first pair of legs is a little protuberant.

Legs 1-4 have the same spine and setal formula as in the male of *K. regalis*. The exopods of these legs are very similar in details to those of *K. regalis*. The endopod of leg 1 (fig. 50), with the formula I, I, 4 on the last segment, is not geniculate, and the inner of the two spines on the last segment is the shorter and is finely barbed. The last segment of the endopod of leg 2 (fig. 51) is much like that of the female, and the erect spiniform process seen in *K. regalis* is absent. The endopods of legs 3 and 4 are like those in the female.

Leg 5 (fig. 52) has a small slender unornamented free segment $22 \times 7\text{ }\mu\text{m}$. Terminally the outer seta is $30\text{ }\mu\text{m}$ long, the inner spine $20\text{ }\mu\text{m}$, both naked. The seta on the body near the free segment is $28\text{ }\mu\text{m}$ and naked.

Leg 6 (fig. 53) consists of the usual posteroventral flap on the genital segment bearing two naked setae 37 μ m and 45 μ m in length and near their insertions a small spiniform process.

The spermatophore, attached to the female in pairs, is 84×43 μ m, not including the neck, and is similar in form to that of *K. regalis*.

The colour in life resembles that of *K. regalis*.

DISCUSSION. This species was originally described from a single female as *Pseudanthessius pectinatus* by A. Scott (1909). Gurney (1927) transferred it to his new genus *Kelleria*. The male has been unknown until now.

Although it is impossible to learn the exact nature of certain structures from A. Scott's description and figures, the similarities with the Madagascan specimens have led us to conclude that our material from Nosy Bé represents *Kelleria pectinata*. Among the striking similarities in the female are : the form of the second antenna and its terminal elements, the nature of the mandible, and the armature of the maxilliped, especially on the last segment.

The female described by A. Scott was a little longer (1.35 mm.) than the Madagascan specimens. His description and figures of the genital segment, the caudal ramus, and leg 5, though rather cursory, suggest resemblances with our material. His figure Pl. LXVIII, fig. 25, of the second maxilla, shows a somewhat different number and arrangement of the spines on the short lash. Since variation in these spines exists in *Kelleria* (compare our figs. 13 and 14 of *K. regalis*), it is very possible that A. Scott's description of the spines in his single female may represent individual variation.

A. Scott's female was found in surface plankton in the Bali Sea, $8^{\circ} 0' 3''$ S, $116^{\circ} 59' 0''$ E. Our specimens from Madagascar occurred in intertidal burrows of unknown origin, except for one collection from burrows of the shrimp *Axius acanthus*. Frequently *K. regalis* and *K. pectinata* occurred together in the same burrows. Often these two species of *Kelleria* inhabited burrows in which *Hemicyclops* also lived. In one collection (that at Ampassipohe, May 11, 1964) both species of *Kelleria* were found in company with *Hemicyclops diremptus* Humes, 1965, *H. carinifer* Humes, 1965, and *H. biflagellatus* Humes, 1965. In another collection (that at Nosy Roty, May 12, 1964) *K. pectinata* occurred with *H. carinifer*, *H. diremptus*, and *H. kombensis* Humes, 1965. In still another (that from *Axius* burrows at Andilana, October 8, 1960) *K. pectinata* occurred with *H. axiophilus* Humes, 1965, and *H. amplicaudatus* Humes, 1965.

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PLATE I

Kelleria regalis Gurney, 1927, female

- FIG. 1. Dorsal (A)
- FIG. 2. Urosome, dorsal (B)
- FIG. 3. Area of attachment of egg sac, dorsal (C)
- FIG. 4. Area of attachment of egg sac, lateral (C)
- FIG. 5. Caudal ramus, dorsal (D)
- FIG. 6. Rostrum and first antenna, anteroventral (E)

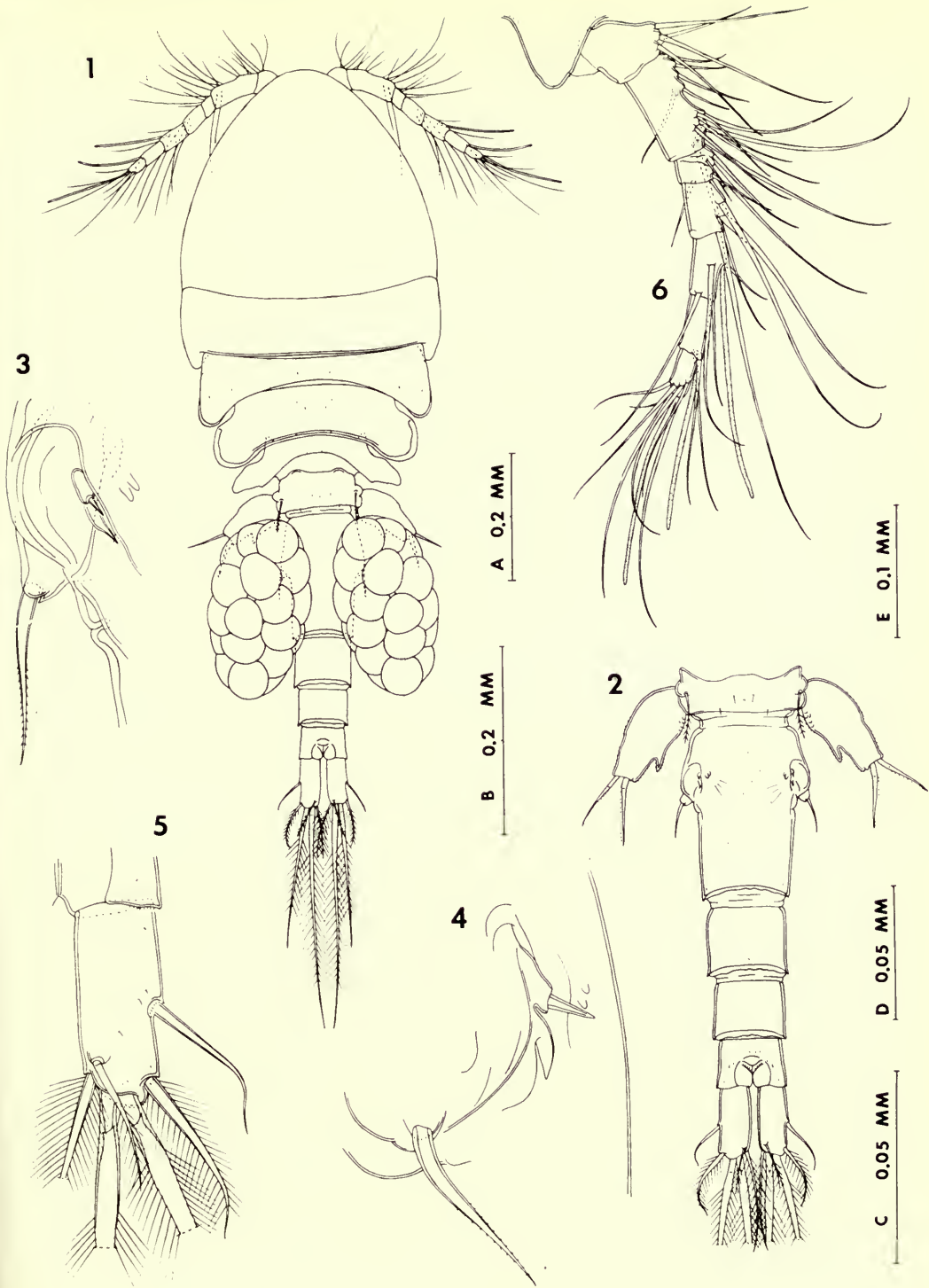


PLATE 2

Kelleria regalis Gurney, 1927, female

- FIG. 7. Profile of rostrum (R) and labrum (L), lateral (E)
- FIG. 8. Second antenna, anterior (F)
- FIG. 9. Labrum, ventral (F)
- FIG. 10. Mandible, posterior (D)
- FIG. 11. Paragnath, anterior (D)
- FIG. 12. First maxilla, anterior (D)
- FIG. 13. Second maxilla, posterior (D)
- FIG. 14. Abnormal second segment of second maxilla, posterior (D)
- FIG. 15. Maxilliped, inner (F)

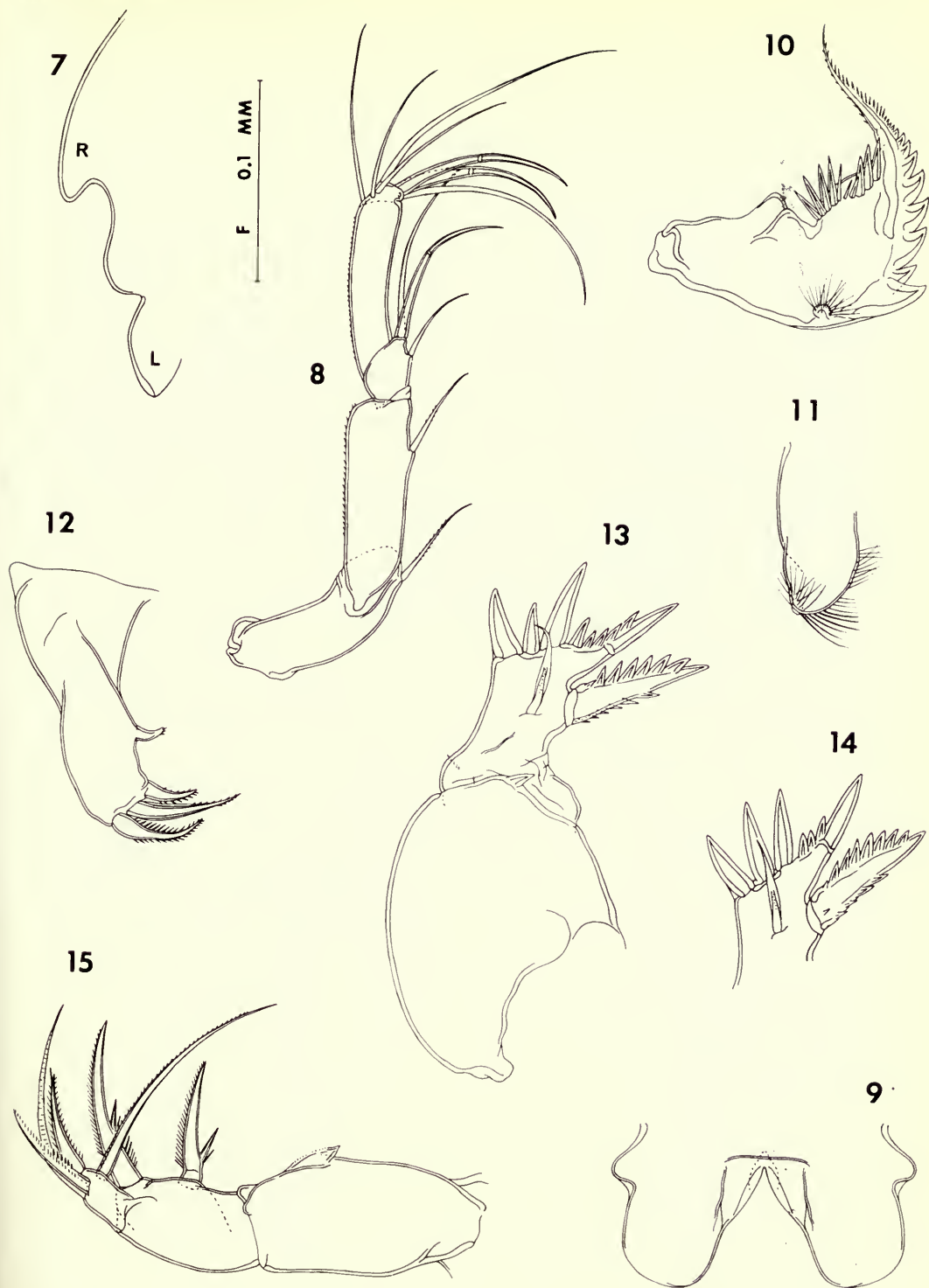


PLATE 3

Kelleria regalis Gurney, 1927, female

- FIG. 16. Leg 1 and intercoxal plate, anterior (F)
FIG. 17. Leg 2, anterior (F)
FIG. 18. Leg 3, anterior (F)
FIG. 19. Leg 4 and intercoxal plate, anterior (F)

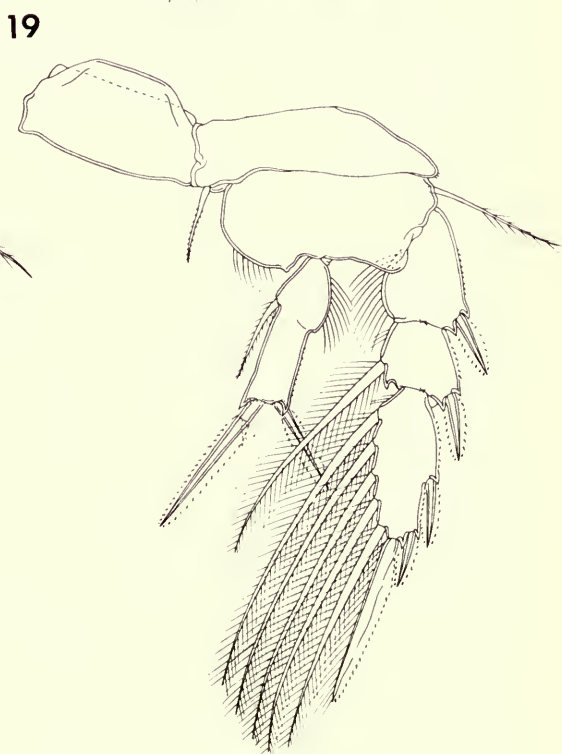
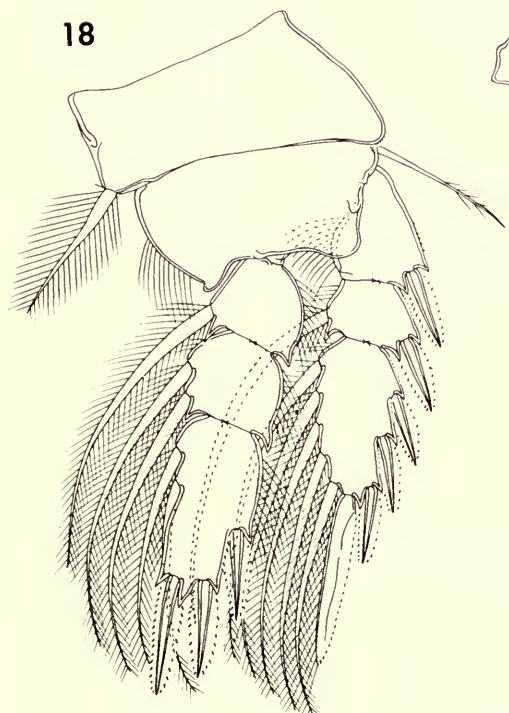
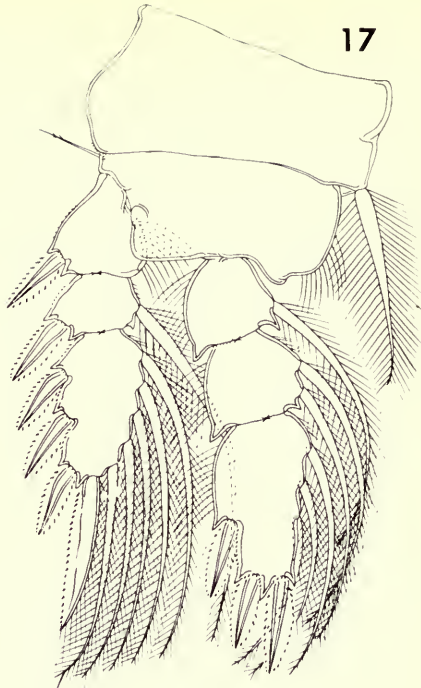
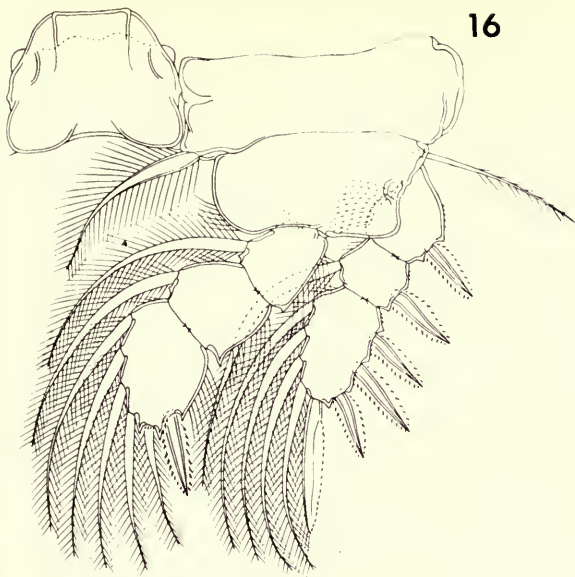


PLATE 4

Kelleria regalis Gurney, 1927, female

FIG. 20. Leg 5, dorsal (D)

FIG. 21. Abnormal free segment of leg 5, dorsal (D)

Kelleria regalis Gurney, 1927, male

FIG. 22. Dorsal (A)

FIG. 23. Urosome, dorsal (E)

FIG. 24. Second maxilla, posterior (D)

FIG. 25. Maxilliped, outer (F)

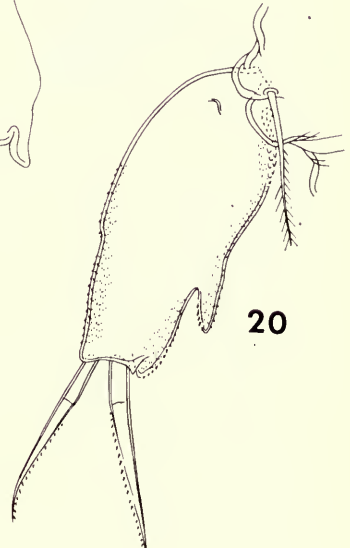
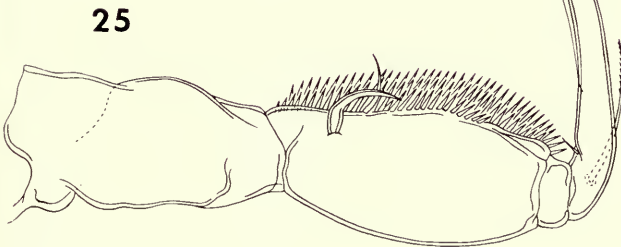
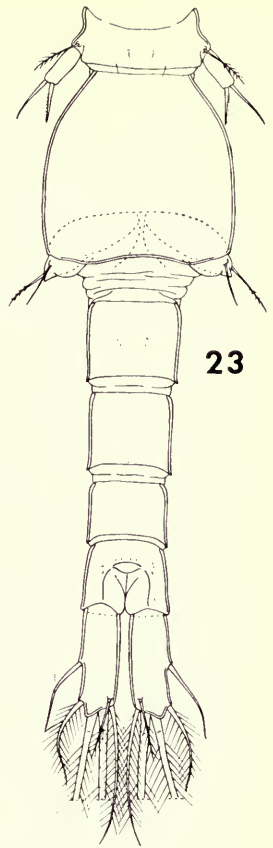
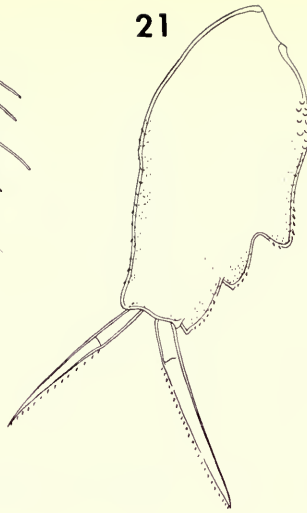
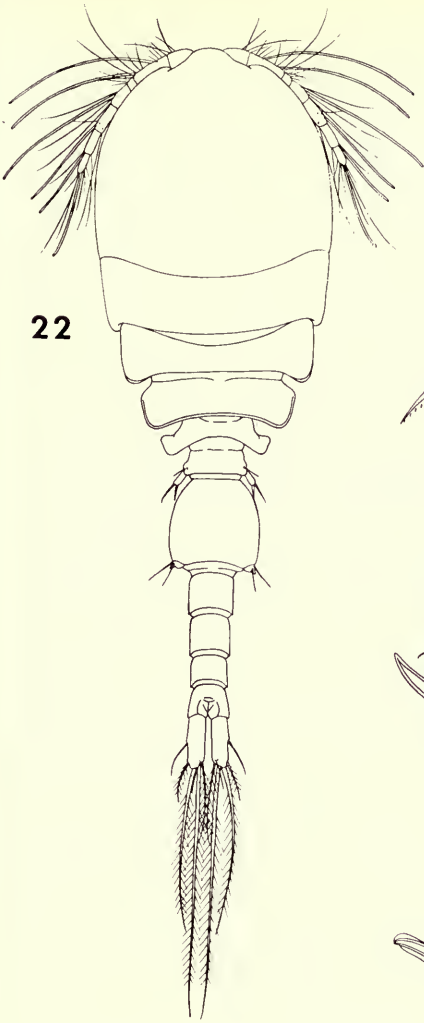


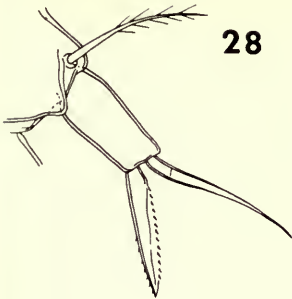
PLATE 5

Kelleria regalis Gurney, 1927, male

- FIG. 26. Endopod of leg 1, anterior (D)
- FIG. 27. Third segment of endopod of leg 2, anterior (D)
- FIG. 28. Leg 5, dorsal (D)
- FIG. 29. Leg 6, ventral (D)
- FIG. 30. Spermatophores, attached to female, dorsal (F)

Kelleria pectinata (A. Scott, 1909), female

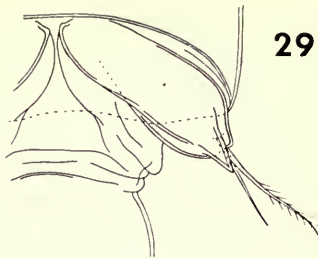
- FIG. 31. Dorsal (A)



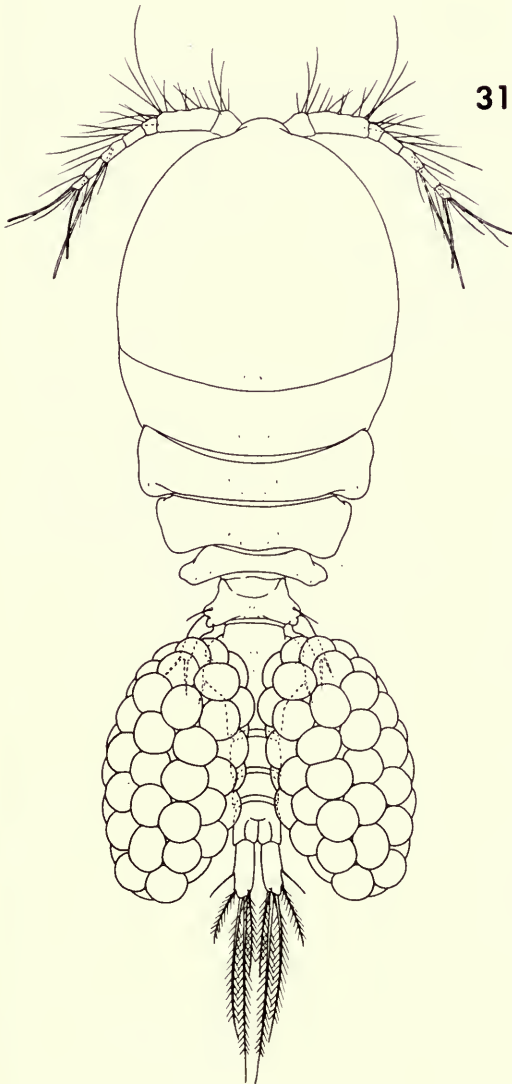
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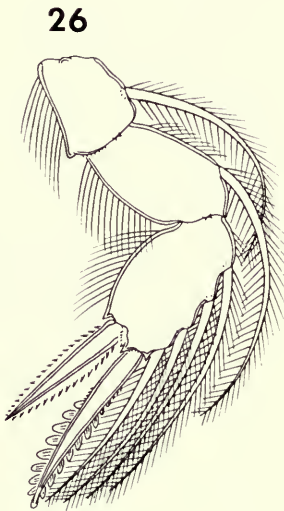
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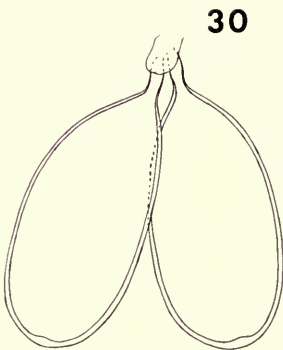
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PLATE 6

Kelleria pectinata (A. Scott, 1909), female

- FIG. 32. Urosome, dorsal (E)
- FIG. 33. Area of attachment of egg sac, dorsal (c)
- FIG. 34. Caudal ramus, dorsal (c)
- FIG. 35. Second antenna, anterior (D)
- FIG. 36. Mandible, posterior (c)
- FIG. 37. First maxilla, posterior (c)
- FIG. 38. Second maxilla, posterior (D)

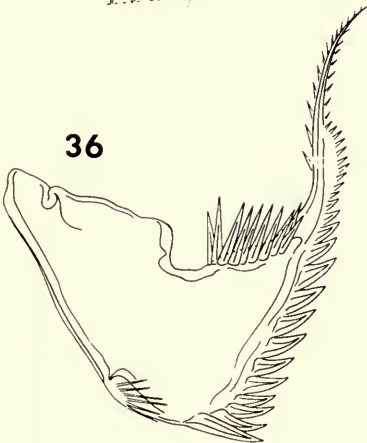
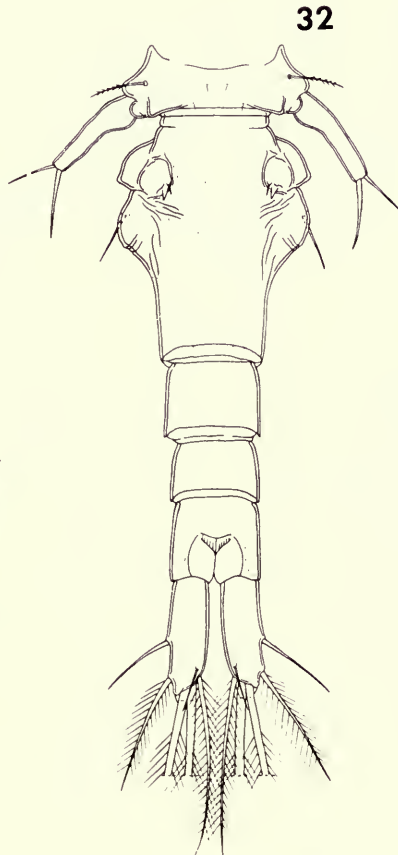
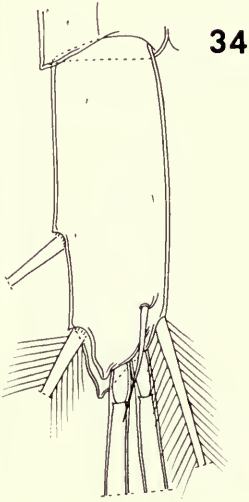
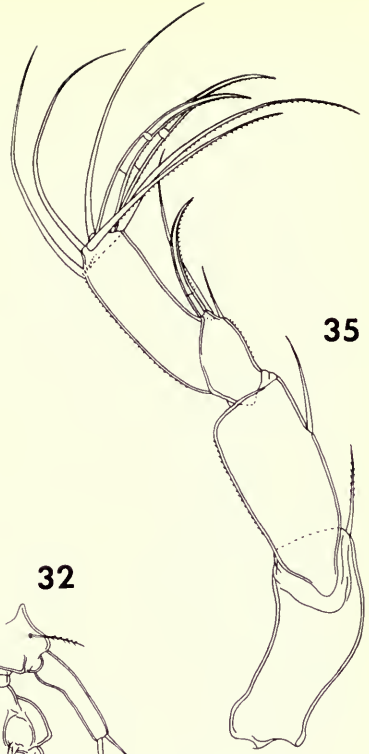
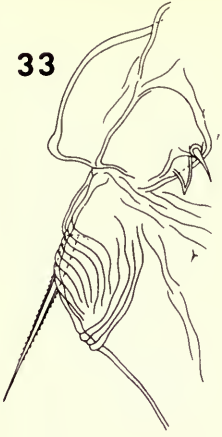


PLATE 7

Kelleria pectinata (A. Scott, 1909), female

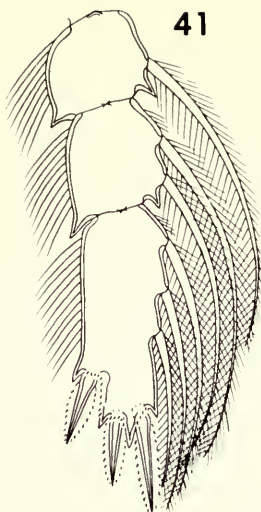
- FIG. 39. Maxilliped, inner (F)
- FIG. 40. Endopod of leg 1, anterior (D)
- FIG. 41. Endopod of leg 2, anterior (D)
- FIG. 42. Third segment of endopod of leg 3, anterior (D)
- FIG. 43. Leg 4, anterior (D)
- FIG. 44. Leg 5, dorsal (C)

Kelleria pectinata (A. Scott, 1909), male

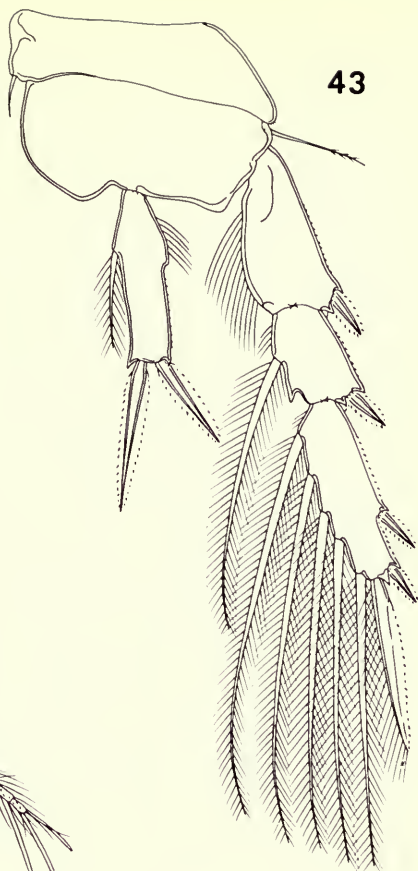
- FIG. 45. Dorsal (A)



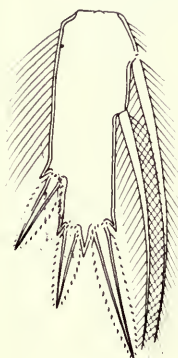
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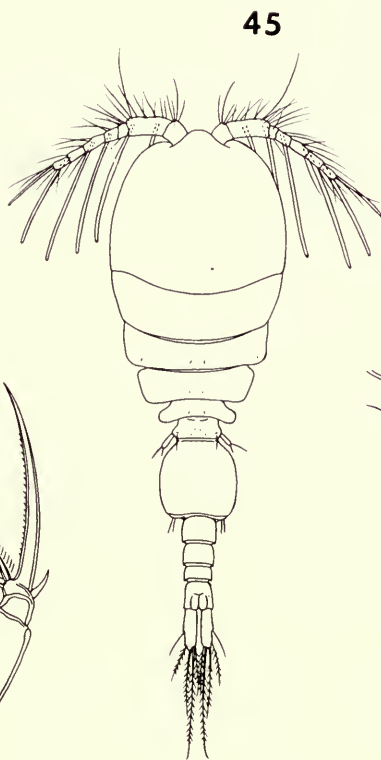
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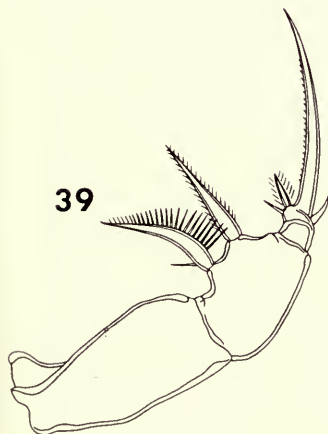
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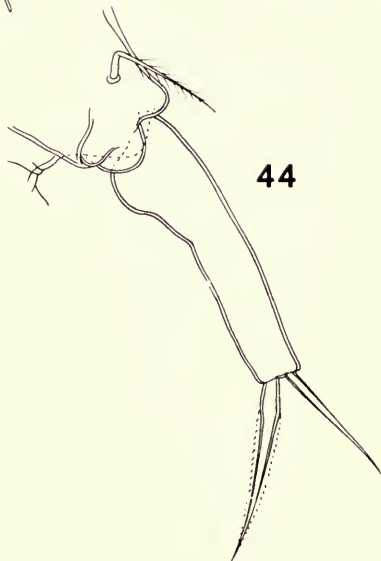
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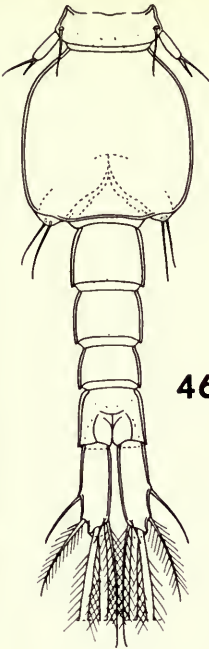


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PLATE 8

Kelleria pectinata (A. Scott, 1909), male

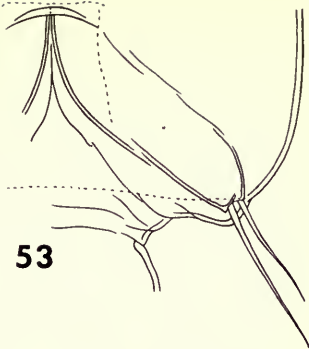
- FIG. 46. Urosome, dorsal (E)
- FIG. 47. Paragnath, anterior (c)
- FIG. 48. Second maxilla, posterior (c)
- FIG. 49. Maxilliped, inner (D)
- FIG. 50. Endopod of leg 1, anterior (c)
- FIG. 51. Third segment of endopod of leg 2, anterior (c)
- FIG. 52. Leg 5, dorsal (G)
- FIG. 53. Leg 6, ventral (c)



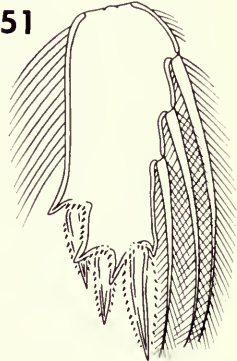
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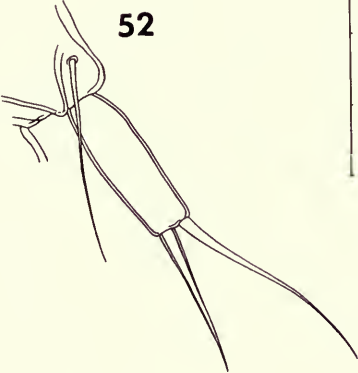
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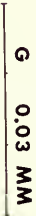
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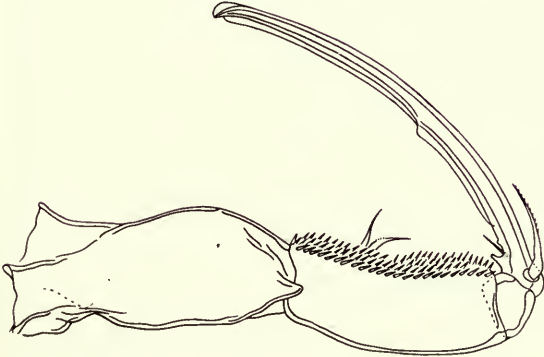
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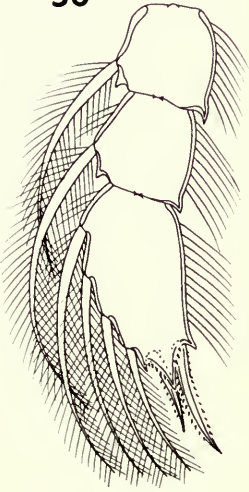
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A REVIEW OF THE IGUANID
LIZARD GENUS *ENYALIUS*



R. ETHERIDGE

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ZOOLOGY

Vol. 18 No. 8

LONDON : 1969

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A REVIEW OF THE IGUANID LIZARD GENUS *ENYALIUS*

By RICHARD ETHERIDGE

SYNOPSIS

The external morphology, distribution, and systematics of the iguanid lizard genus *Enyalius* are reviewed. Eight species are recognized, one of them described here as new. *Enyalius* is compared with *Enyalioides*, *Anisolepis*, and *Aptycholaemus*, and a key is given to the species of *Enyalius*.

INTRODUCTION

Enyalius is a genus of arboreal iguanid lizards that inhabits forested areas in eastern South America. It has remained rare in the collections of North American museums, but during a recent tour of European museums I was able to examine excellent series of most of the species that have been described. Although many of these collections were made during the latter part of the last and the early part of the present century no attempt has been made to review the genus since Boulenger's (1885b) *Catalogue of the Lizards in the British Museum*. On the basis of these collections, and the few specimens available in North America, I have undertaken a review of the genus. Its purpose is to define and characterize the genus *Enyalius*, compare it with those genera to which it appears to be allied, and present characterizations and synonymies of the species. Unfortunately most of the specimens examined have only very general or imprecise locality data so that the exact geographical distribution of the species cannot be determined. Little has been published on the colour of living animals, or on their habits. Therefore a generic revision in the "modern" sense cannot yet be attempted.

The first species now known under the generic name *Enyalius* was described by Wied (1821 : 247) as *Agama catenata*. Three species described by Spix (1825 : 9-11) as *Lophyrus rhombifer*, *L. margaritaceus*, and *L. albomaxillaris* all appear to be referable to Wied's *Agama catenata*.

A second form described by Wied (1825 : 125) as *Agama picta* has been placed in the genera *Ecpymotes* (Fitzinger, 1826 : 49), *Uraniscodon* (Kaup, 1826 : 91 ; 1827 : 612 ; Gray, 1845 : 223), *Hypsibatus* (Wagler, 1830 : 150 ; Wiegmann, 1834 : 15 ; Fitzinger, 1843 : 58), *Ophryessa* (Gray, 1831 : 40), *Calotes* (Schinz, 1835 : 86), and *Uperanodon* (Duméril & Bibron, 1837 : 251). Boulenger (1885b : 179) placed this form in the synonymy of *Uraniscodon* (= *Plica*) *umbra*, and this allocation has been followed by all subsequent authors. Wied's *Agama picta* is nevertheless a valid

species of *Enyalius*. The same species was described as *Enyalius zonatus* by Wettstein (1926 : 1).

Lesson (1828 : 32) described *Lophyrus brasiliensis*, a valid species of *Enyalius* that has been considered by Boulenger (1885b : 118) and all subsequent authors to be a synonym of *Enyalius catenatus*.

In 1830 Wagler proposed the generic name *Enyalius* for *Agama catenata* and *Lophyrus margaritaceus*. Up to this time the generic names that had been applied to species of this genus were *Agama* (Wied, 1821 : 247 ; 1825 : 125), *Lophyrus* (Spix, 1825 : 9-11 ; Lesson, 1828 : 32), *Ecphymotes* (Fitzinger, 1826 : 49), and *Uraniscodon* (Kaup, 1826 : 90-91). All of these generic names are unavailable for *Agama catenata*. Fitzinger (1843 : 16) designated *Agama catenata* Wied as the type species of *Hypsibatus* (*Enyalius*).

Duméril & Bibron (1837 : 234) described *Enyalius bilineatus*, a species that has until now been known under the name *Enyalius fitzingeri*. The error dates from Boulenger (1885b : 121) who adopted Wiegmann's (1834 : 47) name *Laemanctus fitzingeri* for the species, a name which Wiegmann based upon a specimen of *Anisolepis undulatus*. Duméril & Bibron (1837 : 231) also referred several specimens to *Enyalius rhombifer*, one of which is a specimen of *Enyalius brasiliensis*, and the other two of which represent an as yet unnamed species described later in this paper.

Boulenger described two additional species of *Enyalius* : *iheringii* (1885a : 192), and *bibronii* (1885b : 119). Boulenger (1885b : 112) also described the genus *Enyalioides* for a number of species that had until that time been included in *Enyalius*. All of the previously described species that he transferred to *Enyalioides* properly belong there, but his new species, *Enyalioides leechii* described in the same work (1885b : 473) is actually a species of *Enyalius*.

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The following abbreviations are used :

A.M.N.H.	American Museum of Natural History, New York.
B.M.N.H.	British Museum (Natural History), London.
C.A.S.	California Academy of Sciences, San Francisco.
F.M.N.H.	Field Museum of Natural History, Chicago.
M.C.Z.	Museum of Comparative Zoology, Harvard University, Cambridge (Massachusetts).
M.H.N.P.	Muséum National d'Histoire Naturelle, Paris.
M.V.Z.	Museum of Vertebrate Zoology, University of California, Berkeley.
M.Z.T.	Istituto e Museo de Zoologia della Università di Torino, Torino.
N.M.W.	Naturhistorischen Museum, Wien.
S.M.F.	Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main.
U.S.N.M.	United States National Museum, Washington.
Z.M.H.	Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg.
Z.M.K.	Zoologiske Museum, København.
Z.S.B.S.	Zoologisches Sammlung des Bayerischen Staates, München.

ENYALIUS Wagler, 1830, Nat. Syst. Amph., p. 150.

TYPE SPECIES *Agama catenata* Wied., by designation (Fitzinger, 1843 : 16).

DIAGNOSIS. *Enyalius* is a member of that group of iguanid lizards in which the anterior inscriptional ribs extend from the distal ends of the dorsal ribs to the ventral midline, where they join one another to form continuous chevrons, and the posterior inscriptional ribs either form chevrons that are unattached to the dorsal ribs, or are absent (Etheridge, 1965 : 163-166). Within this group *Enyalius* differs from the anoles (*Anolis*, *Chamaeleolis*, *Chamaelinorops*, *Phenacosaurus*, *Tropidodactylus*) in lacking both transversely expanded subdigital lamellae and an extensile gular fan ; a few anoles lack one or the other of these features, but never both. *Enyalius* differs from *Enyalioides*, *Hoplocercus*, and *Morunasaurus* in having a small nasal scale with a laterally oriented nostril ; the nasal scale is very large and the nostril is posterolaterally oriented in the latter three genera (Fig. 11). *Enyalius* differs from *Leiosaurus*, *Diplolaemus*, *Aperopristsis*, *Pristidactylus*, and *Cupriguanus* in having a compressed body, longer digits and longer limbs, and a longer tail. *Enyalius* differs from *Polychrus* in lacking femoral pores, and from *Urostrophus*, *Anisolepis*, and *Aptycholaemus* in having a row of enlarged scales aligned middorsally.

CHARACTERISTICS. Upper head scales polygonal and juxtaposed, smooth and flat or convex, or convex and keeled. Supraorbital semicircles each with 9 to 15 scales somewhat larger and more strongly convex than those adjacent, medially separated

between the orbits by two or three scales. Supraoculars small laterally, enlarged medially and centrally, the largest equal to, to much smaller than scales of supra-orbital semicircles. Interparietal scale small, a little larger than parietals, with a distinct "eye". Nasal scales small, strongly convex, below the canthal ridge, with a large, laterally oriented nostril. Canthal ridge distinct, with one or two large, overlapping scales. Seven to 14 superciliaries, the first few elongate with oblique sutures, the remainder squarish with vertical sutures. Loreal scales polygonal and juxtaposed, smooth or keeled. Orbit bordered in front and below by an arc of large scales, keeled along their upper border or with a median keel, subequal or one of them conspicuously elongate below the eye. Upper labials more or less rectangular, separated from loreals by several irregular rows of very small scales, and from suboculars by one or two rows of scales. Temporals usually polygonal and juxtaposed, smooth and flat or convex, or obtusely keeled, those overlying supratemporal arcade somewhat enlarged. Lower labials similar to upper labials. Lateral gulars polygonal and juxtaposed, smooth and convex, grading medially into smaller, rounded, convex, smooth or keeled scales with granules in the interspaces, and posteriorly becoming abruptly larger and imbricate in front of gular fold.

A middorsally aligned row of vertebral scales present, enlarged and forming a serration or crest down the middle of the back in all species save one. Dorsal and lateral nuchal scales small, convex, and granular. Dorsal scales of body adjacent to vertebral row polygonal, juxtaposed, of various sizes, smooth or obtusely keeled, laterally grading into smaller, rounded, convex scales with more or less triangular granules in between. Ventral scales of body several times larger than dorsals, arranged more or less in transverse rows, smooth or keeled.

Tail long and slender, from about one and a half to nearly three times longer than the head and body together, slightly compressed at its base, rounded for most of its length. Caudal vertebrae autotomic or not, when autotomic caudal scales arranged in segments that correspond to autotomic segments of vertebral column, with five to seven dorsal and three ventral scale rows in each segment (Fig. 10C); when caudal vertebrae are not autotomic caudal scales arranged irregularly with no trace of segmentation (Fig. 10A).

Dorsal scales of forelimb and of antibrachium rhomboidal, somewhat larger than body scales, subimbricate to imbricate, smooth or obtusely keeled. Ventral scales of brachium small, convex, and juxtaposed. Posterior surface of thigh covered with small, convex, juxtaposed scales that continue up onto the dorsal surface of the thigh to about midway along the femoral axis. Remainder of hind limb covered with large, rhomboidal, subimbricate to imbricate, smooth or obtusely keeled scales. Subdigital lamellae smooth and convex, or slightly or distinctly keeled; if smooth a median longitudinal groove divides distal four or five lamellae of each digit.

A distinct transverse gular fold enclosing granular scales present, ascending on each side of neck in front of forelimb, and curving back over forelimb insertion, fading out on shoulder or at some point further back along side of body. No femoral or preanal pores.

Pattern highly variable, but basically brownish (in preservative) above, with a pair of light paravertebral stripes and alternating light and dark crossbands. Pattern

variously modified by loss of paravertebral stripes or crossbands, constriction or interruption of crossbands by stripes, alternation of crossbands, etc. Males without a pattern, or pattern of reduced intensity in some species.

***Enyalius bilineatus* Duméril & Bibron**

Enyalius bilineatus Duméril & Bibron, 1837, p. 234.

Hypsibatus (Dryophilus) bilineatus Fitzinger, 1843, p. 57.

Enyalius fitzingeri Boulenger, 1885b, p. 121.

HOLOTYPE. M.H.N.P. No. 6817, from "Brésil".

CHARACTERISTICS. (Fig. 1). The dorsal head scales are smooth and flat. Several rows of enlarged supraoculars are partly or completely separated from the

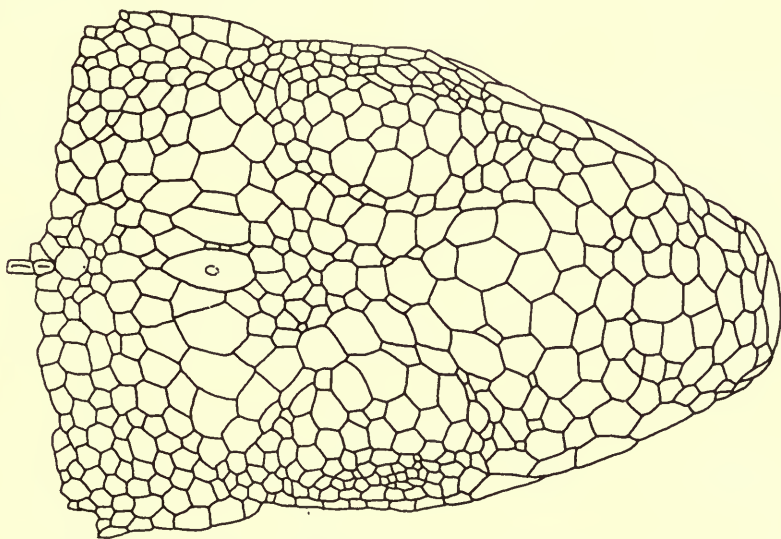


FIG. 1. Dorsal view of the head of *Enyalius bilineatus* (Z.M.K. No. 5).

supraorbital semicircles by a row of small circumorbitals, and grade laterally into several rows of much smaller scales. The largest supraoculars are about equal in size to the scales of the supraorbital semicircles. The distance between the nasal scale and the tip of the snout is about one-half the distance between the nasal and anterior corner of the orbit. The orbit is usually bordered below by an elongate scale, preceded by two shorter, but otherwise similar scales, all of which have a keel along their upper margins. Occasionally the orbit is bordered in front and below by an arc of four subequal scales. The temporals are polygonal, juxtaposed, and keeled.

A vertebral row of enlarged, keeled scales extends from the occiput to the base of the tail, forming a low serration down the middle of the back. The dorsal scales adjacent to the vertebral row are polygonal, subimbricate, distinctly keeled, and of

TABLE I

Species	Sex	N	Vertebral Scales	Paravertebral Scales	Midbody Scales
<i>bilineatus</i>	F	19	46-(59.3)-74	94-(114.4)-130	81-(93.8)-106
	M	8	53-(62.1)-71	98-(116.4)-132	85-(96.6)-104
<i>pictus</i>	F	2	47-(47.5)-48	153-(159.5)-166	146-(147.0)-148
	M	3	43-(50.0)-59	153-(155.5)-157	154-(160.0)-166
<i>bibronii</i>	F	2	61-(63.5)-66	135-(147.0)-159	102-(125.0)-149
<i>catenatus</i>	F	14	40-(48.6)-61	125-(145.2)-163	130-(143.0)-164
	M	9	45-(50.1)-58	130-(146.3)-164	132-(142.0)-165
<i>iheringii</i>	F	72	40-(47.9)-61	100-(115.7)-131	102-(117.4)-136
	M	35	40-(46.6)-58	91-(110.8)-130	103-(117.6)-130
<i>brasiliensis</i>	F	3	45-(46.3)-48	130-(138.3)-149	152-(156.0)-162
	M	5	47-(49.2)-51	146-(149.2)-154	146-(151.5)-160
<i>boulengeri</i>	F	20	33-(38.5)-43	123-(138.7)-162	110-(127.4)-145
	M	7	34-(37.6)-41	127-(138.8)-157	116-(128.4)-142
<i>leechii</i>	F	1	Not applicable	143	140

Some scale counts for the species of *Enyalius*. Vertebral and paravertebral scales are counted from the occiput to a line even with the anterior border of the hind limb at right angles to the trunk; midbody scales are counted halfway between the limb insertions. N = number of specimens examined. Mean figures are in parentheses.

various sizes. Laterally they grade into somewhat smaller and more convex but otherwise similar scales. The ventral scales are large and sharply keeled, the keels forming parallel, longitudinal rows. Scales counts are given in Table I.

The tail is not autotomic. The caudal scales are arranged in irregular rows with

TABLE II

Species	Sex	N	Max. s-v	Tail/Snout-vent
<i>bilineatus</i>	F	10	105	2.62-(2.92)-3.31
	M	9	88	2.92-(3.12)-3.30
<i>pictus</i>	F	1	111	1.96
	M	3	106	2.09-(2.12)-2.17
<i>bibronii</i>	F	1	100	1.86
<i>catenatus</i>	F	11	107	1.98-(2.20)-2.34
	M	10	107	2.13-(2.20)-2.36
<i>iheringii</i>	F	54	124	1.94-(2.08)-2.37
	M	25	100	2.01-(2.15)-2.25
<i>brasiliensis</i>	F	2	105	2.04-(2.06)-2.08
	M	3	85	2.05-(2.19)-2.50
<i>boulengeri</i>	F	22	117	1.59-(1.71)-1.92
	M	7	107	1.72-(1.79)-1.86
<i>leechii</i>	F	1	105	1.75

Maximum size in millimetres snout-vent length (Max. s-v), and variation in the ratios of tail length divided by snout-vent length (Tail/Snout-vent) in the species of *Enyalius*. N = number of specimens used in calculation of tail/snout-vent ratios. Note: Males of *bibronii* and *leechii* are unknown.

no trace of segmentation (Fig. 9A). Variation in snout-vent length to tail length ratios, and maximum adult sizes of both sexes are given in Table 2.

The subdigital lamellae are smooth and convex, the distal four or five lamellae of each digit medially divided. The fourth toe of the adpressed hind limb reaches a point between the orbit and the tip of the snout.

Colour in preservative : The head is a uniform light brown above. A wide, dark brown band extends from in front of the eye back along the side of the neck, becoming wider, and ending abruptly just in front of the shoulder. Bordering the brown band below is a narrow, cream line that passes from the posterior canthal scale back along the suboculars, through the ear, and ends at the insertion of the forelimb, and bordering it above is a wide, cream band that begins at the upper corner of the orbit and extends back on the neck and body as a paravertebral stripe, ending on the base of the tail. Usually three or four wide, dark brown, cream edged bands cross the back, constricted or interrupted where they cross the paravertebral light stripes. The tail has a dorsal series of dark brown, cream edged ovals. The limbs are light brown with a few bold, dark brown, cream edged bands or spots. The ventral surfaces are whitish, with three wide, grey stripes (one median, two lateral) that begin near the jaw symphysis and extend to the vent.

In both sexes the colour pattern is usually as described above. In some individuals the dark crossbands are lacking ; in others the light paravertebral stripes are lacking. I have seen no specimens in which both crossbands and stripes are absent.

REMARKS. The holotype appears to have been stored for a time in strong preservative, or to have been partly desiccated. The extremities are somewhat shrivelled, and the subdigital lamellae appear wrinkled. The lamellae are, however, perfectly smooth surfaced, although in the type description they are said to be keeled.

Enyalius bilineatus has been known since Boulenger (1885b : 121) under the name *Enyalius fitzingeri*. In the genus *Laemactus* Wiegmann (1834 : 46) briefly described three Brazilian species : *fitzingeri*, *undulatus*, and *obtusirostris*, and gave a lengthy description of a fourth species, *longiceps*, from México. Duméril & Bibron (1837 : 72-76) repeated the descriptions on Wiegmann's authority, and added a fifth species *L. acutirostris*. Fitzinger (1843) overlooked *obtusirostris*, but placed several additional species in *Laemactus* : *fitzingeri*, *undulatus*, and *vautieri* were placed in the subgenus *Urostrophus*, with *vautieri* designated (p. 16) as the type of the subgenus. Gray (1845 : 184-185) placed *fitzingeri*, *undulatus*, *obtusirostris*, and *acutirostris* under the genus *Ecphymotes*, basing his description entirely on Wiegmann. Boulenger (1885b : 121) recognized *fitzingeri* and *undulatus* as species of *Enyalius*, and included *obtusirostris* in the synonymy of *undulatus*. On the following page he described a new species of *Anisolepis*, *A. iheringii*, but in the " addenda and corrigenda " (vol. 3 : 500-501) *undulatus* was transferred to the genus *Anisolepis*, and *A. iheringii* was placed in its synonymy.

I have examined Wiegmann's holotypes of his species of *Laemactus*, and find that those of *fitzingeri* (Z.M.B. 495), *obtusirostris* (Z.M.B. 496), and *undulatus* (Z.M.B. 497) are all of the same species, that which is presently known as *Anisolepis undulatus*. However, it is clear from Boulenger's characterization of *Enyalius fitzingeri* (and my examination of his specimens : B.M.N.H. Nos. 49.11.29.2 and 61.5.21.3)

that the species to which he is referring is *Enyalius bilineatus*, which he included in the synonymy of *E. catenatus*.

RANGE. *Enyalius bilineatus* is known from the states of Espírito Santo and adjacent eastern Minas Gerais, Brazil. *E. catenatus*, *E. boulengeri*, and *E. bibronii* all probably occur within the range of *E. bilineatus* (Fig. 10).

SPECIMENS EXAMINED. Brazil: Minas Gerais, Antônio Carlos M.C.Z. 84034; Minas Gerais, Viçosa Muías M.V.Z. 14941; Minas Gerais, no specific locality M.C.Z. 5567; Espírito Santo, Santa Theresa, S.M.F. 24890; Espírito Santo, no specific locality N.M.W. 12968 (8 exs), S.M.F. 11054, Z.M.H. 2216 (16 exs); between Espírito Santo and Minas Gerais Z.M.H. 2206 (13 exs), 2207 (9 exs); Ribeirão de Rapozo Z.M.K. 25; Lagoa Santa Z.M.K. 26-29; no specific locality M.H.N.P. 6817 (holotype), B.M.N.H. 61.5.21.3, 49.11.29.2.

Enyalius pictus (Wied)

Agama picta Wied, 1825, p. 125.

Ecphymotes pictus Fitzinger, 1826, p. 49.

Uraniscodon picta Kaup, 1826, p. 91.

Uraniscodon (Pneustes) picta Kaup, 1827, p. 612.

Hypsibatus picta Wagler, 1830, p. 150.

Ophyesa Picta Gray, 1831, p. 40.

Calotes pictus Schinz, 1835, p. 86, pl. 25, fig. 2.

Uperanodon pictum Duméril & Bibron, 1837, p. 251.

Hypsibatus (Uperanodon) pictus Fitzinger, 1843, p. 48.

Uraniscodon pictum Gray, 1845, p. 223.

Enyalius zonatus Wettstein, 1926, p. 1.

HOLOTYPE. The holotype of *Enyalius pictus* has not been located but apparently was in the American Museum of Natural History, New York, and is now lost. In the files of the museum is a catalogue, dated 1860, that lists all of the specimens of Wied acquired by the American Museum. The holotype of both *Agama catenata* and *Agama picta* are listed, but I can find no record of the latter ever having been catalogued into the American Museum's collection. The origin of the specimen is not specified, but Wied (1825: 129) later stated that specimens were found at Lago d'Arara and Mucurí, which, according to the map of Wied's journeys (Wied, 1820) are in southeastern Bahia: Mucurí a town at the mouth of the Río Mucurí, and Lago d'Arara a few kilometres inland. I therefore propose that the type locality of *Agama picta* be restricted to Mucurí, southeastern Bahia, Brazil. A specimen in the Naturhistorischen Museum in Vienna (No. 13894) from "Mucuri dist." is here designated as the neotype of *Agama picta* Wied.

CHARACTERISTICS. (Fig. 2). The dorsal head scales are smooth and moderately convex. The scales of the supraocular region are small laterally, enlarged centrally and medially, the largest about three-fourths to as large as the scales of the supra-orbital semicircles. The distance between the nasal scale and the tip of the snout is slightly less than one-half the distance between the nasal and the anterior corner of the orbit. The orbit is bordered in front and below by an arc of nine or ten large

scales, each with a median keel. The temporals are polygonal, smooth, and slightly convex.

A vertebral row of enlarged scales extends from the occiput to midway along the tail ; they are conical on the neck, arched and keeled along the back. The dorsal scales adjacent to the vertebral row are smooth, polygonal, juxtaposed, and of various sizes. Laterally they grade into smooth, rounded, strongly convex scales with very small, more or less triangular granules in the interspaces. The ventral scales are smooth, somewhat convex, and several times larger than the dorsals. Scale counts are given in Table 1.

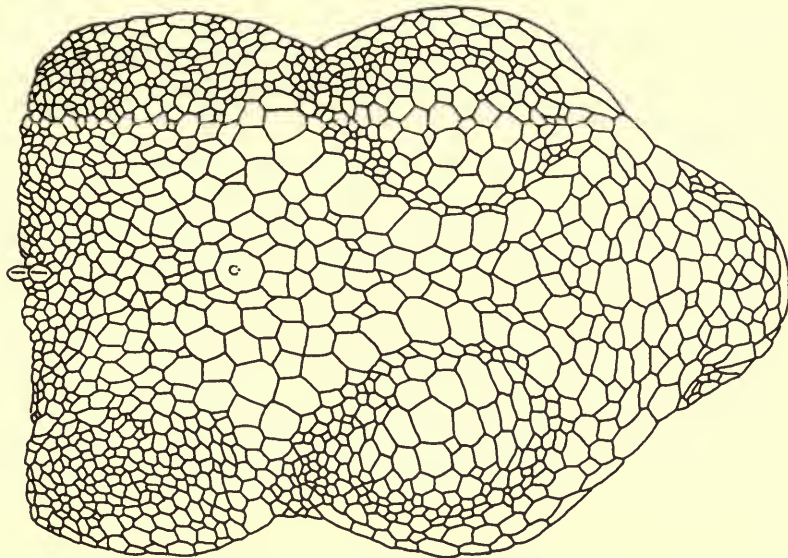


FIG. 2. Dorsal view of the head of *Enyalius pictus* (M.Z.T. No. 2243).

The tail is autotomic, but the caudal scales are arranged in irregular, poorly differentiated segments, usually with six or seven dorsal and three or four ventral scales in each segment (Fig. 9). Variation in snout-vent length to tail length ratios, and the maximum adult size for each sex are given in Table 2.

The subdigital lamellae are smooth and convex, the distal four or five lamellae of each digit medially divided. The fourth toe of the adpressed hind limb extends beyond the tip of the snout.

Colour in preservative : the head and anterior part of the neck is uniform grey. The back and posterior part of the neck are crossed by five wide, brown bands, the first of which is a rich, reddish-brown. Between the brown crossbands are narrow bands of grey, the first of which is conspicuously lighter than the others, almost white. The tail is marked with wide, brown bands, and the limbs with short, brown bars. The ventral surfaces are uniform white. The pattern is equally vivid in both sexes.

REMARKS. The original description of *Agama picta* is detailed, and accompanied

by an excellent coloured illustration, repeated by Schinz (1835 : pl. 25, fig. 2). Its distinctive pattern somewhat resembles the pattern of *Plica umbra*, especially that of more brightly coloured juveniles. It is apparently this resemblance that led workers of the last century to associate the two species in the same or closely related genera. Boulenger (1885b : 179) placed *Agama picta* in the synonymy of *Uraniscodon umbra*, although he, and all authors since Wied, based their treatment of the species entirely upon the original description and illustration. Thus, Wied's *Agama picta* is here referred to the genus *Enyalius* for the first time.

In the Naturhistorischen Museum in Vienna are three specimens of *Enyalius* that correspond exactly to the description and illustration of *Agama picta*. Two of these are the syntypes of *Enyalius zonatus* (Wettstein, 1926 : 1). They are said to have come from Ecuador, and are accompanied only by the additional information that they were donated to the museum by Steindachner in 1905. The third specimen (N.M.W. 13894) was identified in the collection as *Uraniscodon umbra*, and was donated by Steindachner in 1868. The locality label reads "Mucurí district, coll. Wertheimer". The detailed resemblances of these three specimens with the description and illustration of *Agama picta*, and the locality of No. 13894, make it almost certain that they are referable to that species, even though the type is no longer available for comparison, and that the locality of "Ecuador" for *E. zonatus* is in error.

RANGE. *Enyalius pictus* is known only from the vicinity of the type locality, near the mouth of the Río Mucurí in extreme southeastern Bahía, Brazil. *E. catenatus* and *E. bibronii* may be expected in this region also (Fig. 10).

SPECIMENS EXAMINED. Brazil : Bahía, Mucurí N.M.W. 13894 ; no specific locality M.Z.T. 2243. No specific locality : N.M.W. 17188-9 (syntypes of *Enyalius zonatus*, type locality "Ecuador", in error).

Enyalius bibronii Boulenger

Enyalius bibronii Boulenger, 1885b, p. 119.

HOLOTYPE. B.M.N.H. No. 69.11.3.8, from "Bahia", Brazil.

CHARACTERISTICS (Fig. 3). The dorsal head scales are smooth and flat, or moderately convex. The supraoculars are small and numerous laterally, markedly enlarged medially, the largest about equal in size to the scales of the supraorbital semicircles. The distance between the nasal scale and the tip of the snout is less than one-half the distance between the nasal and the anterior corner of the orbit. The orbit is bordered in front and below by an arc of seven or eight large scales, each with a keel along its upper margin. The temporals are smooth and convex, polygonal and juxtaposed except just anterior to the tympanum, where they are rounded with tiny granules in the interspaces.

A vertebral row of enlarged scales extends back from the occiput to the base of the tail, conical on the neck, and arched and keeled along the back. The dorsal scales adjacent to the vertebral row are polygonal, juxtaposed, weakly and obtusely keeled, and of various sizes. Laterally they grade into smooth, rounded, somewhat

convex scales with small, more or less triangular granules in the interspaces. The ventral body scales are several times larger than the dorsals, smooth, except on the chest where they may be faintly, obtusely keeled. Scale counts are given in Table 1.

The tail is autotomic, and the caudal scales are arranged in segments, with six dorsal and three ventral scales in each segment (Fig. 9c). Variation in the snout-vent length to tail length ratio, and the maximum adult size for females (males unknown) are given in Table 2.

The subdigital lamellae are smooth and convex, the distal four or five lamellae of

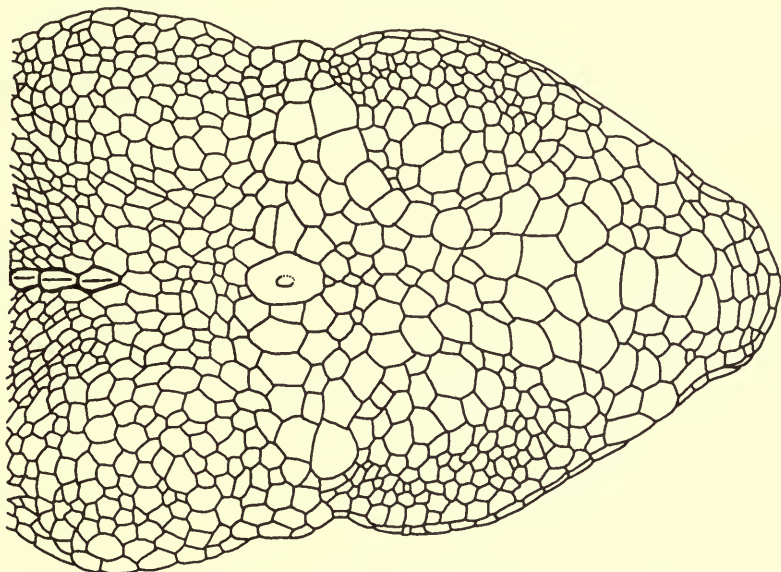


FIG. 3. Dorsal view of the head of *Enyalius bibronii* (B.M.N.H. No. 69.11.3.8, holotype).

each digit medially divided. The fourth toe of the adpressed hind limb extends to the anterior corner of the orbit.

Colour in preservative : the species is known only from two females. The holotype is light greyish-tan above. A short, narrow, brown stripe extends from the eye to the posterior upper labial on each side. A brown $\square$ -shaped mark is present on each side of the head between the orbit and tympanum. A small median, and a pair of larger lateral brown spots are present on the neck. Down the middle of the back is a series of alternating, squarish brown spots, each with a small, round, whitish spot in front and behind. The tail is banded with grey and brown, and the limbs with narrow brown bands. The ventral surfaces are uniform white. The other female has two brown bands across the supraocular region, a wide, dark brown stripe from the eye that extends back through the tympanum and ends abruptly just above the forelimb insertion, bordered below by a narrow, cream stripe. Down the middle of the back is a series of brown ovals, flanked on either side by a yellowish stripe. The undersurfaces are light, cream-yellow with numerous, dark brown spots.

REMARKS. Boulenger (1885b : 119) based *Enyalius bibronii* on a single specimen from Bahía. However, he listed *Enyalius rhombifer* (non Spix) of Duméril & Bibron (1837 : 231) as a synonym, and indicated the range as " Guianas and Brazil ". Three specimens formed the basis of Duméril & Bibron's description of *rhombifer*. One of these is referable to *E. brasiliensis*, and the other two, from Cayenne, are of an unnamed species. Boulenger was apparently misled by the description of *rhombifer* as having smooth ventral scales ; I have examined Duméril & Bibron's specimens, and the ventrals are definitely keeled.

RANGE. *Enyalius bibronii* is known only from an unspecified locality in the state of Bahía, and from Linhares, Espírito Santo, Brazil. *E. catenatus*, *E. bilineatus*, *E. boulengeri*, and *E. pictus* all probably occur within the range of *E. bibronii*. (Fig. 10).

SPECIMENS EXAMINED. Brazil : Bahía ; no specific locality B.M.N.H. 69.11.3.8 (holotype) ; Espírito Santo, Linhares M.C.Z. 82873.

Enyalius catenatus (Wied)

Agama catenata Wied, 1821, p. 247.

Lophyrus Rhombifer Spix, 1825, p. 9.

Lophyrus margaritaceus Spix, 1825, p. 10.

Lophyrus albomaxillaris Spix, 1825, p. 11.

Ophryessa catenata Fitzinger, 1826, p. 48.

Ophryessa margaritaceus Fitzinger, 1826, p. 48.

Uraniscodon rhombifer Kaup, 1826, p. 90.

Uraniscodon margaritaceus Kaup, 1826, p. 90.

Uraniscodon (Ophryessa) catenata Kaup, 1827, p. 612.

Uraniscodon (Ophryessa) margaritacea Kaup, 1827, p. 612.

Enyalius [Agama catenata] Wagler, 1830, p. 150.

Enyalius [Lophyrus margaritaceus] Wagler, 1830, p. 150.

Oph. [yessa] (Xiphurus) Margaritaceus Gray, 1831, p. 40.

Oph. [yessa] (Xiphurus) Rhombifer Gray, 1831, p. 40.

? *Oph. [yessa] (Plica) Braziliensis* (non Lesson) Gray, 1831, p. 40.

Hypsibatus (Enyalius) catenatus Fitzinger, 1843, p. 57.

Hypsibatus (Enyalius) margaritaceus Fitzinger, 1843, p. 57.

Enyalius catenatus Boulenger, 1885, p. 118.

Enyalius catenatus paulista Ihering, 1898, p. 102.

HOLOTYPE. A.M.N.H. No. 108. The original description is given in a footnote in Chapter VII (vol. 2) of Wied's *Reise nach Brasilien* (1821). The chapter is a daily account of Wied's journey from Conquista north to Salvador, the capital city of Bahía. The footnote occurs on page 247 which, together with the preceding page, is concerned with the fauna near Cabeça do Boi, a village just north of the Rio das Contas in eastern Bahía. Cabeça do Boi may thus reasonably be considered the type locality.

CHARACTERISTICS. (Fig. 4). The dorsal head scales are smooth and slightly convex on the snout and in the frontonasal region, faintly to moderately keeled in the frontal and supraocular regions. The supraoculars are small and numerous laterally, enlarged medially ; the largest supraoculars are about three-quarters to as large as the scales of the supraorbital semicircles. The distance between the nasal

scale and the tip of the snout is about one-half the distance between the nasal and the anterior corner of the orbit. The orbit is bordered in front and below by an arc of 10 or 11 enlarged scales, each with a median keel. The temporals are smooth or weakly keeled.

A vertebral row of enlarged scales extends from the occiput to the base of the tail ; they are conical on the neck, and arched and keeled along the back. The dorsal scales adjacent to the vertebral row are polygonal, juxtaposed, faintly keeled, and of various sizes. Laterally they grade into rounded, convex scales with more or less

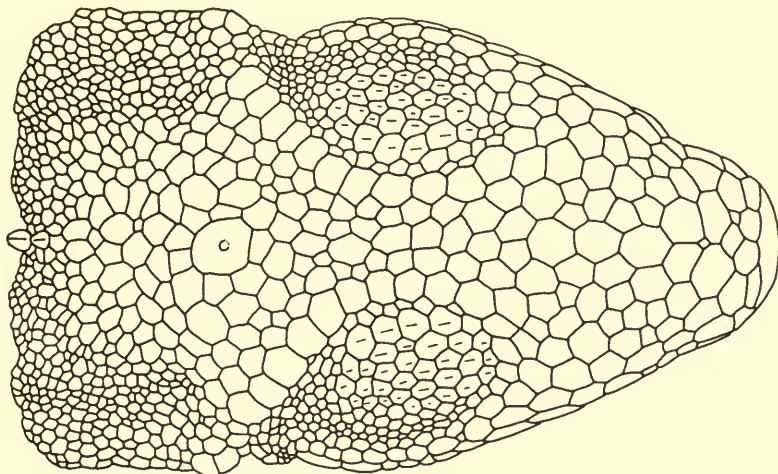


FIG. 4. Dorsal view of the head of *Enyalius catenatus* (M.C.Z. No. 7320).

triangular granules in the interspaces. The ventral scales are large and distinctly keeled. Scale counts are given in Table 1.

The tail is autotomic, and the caudal scales are arranged in segments, with five dorsal and three ventral scale rows in each segment. Variation in the snout-vent to tail length ratios, and the maximum sizes of both sexes are given in Table 2.

The subdigital lamellae are smooth and convex, the distal four or five lamellae of each digit medially divided. The fourth toe of the adpressed hind limb extends beyond the tip of the snout.

Colour in preservative : males are almost uniform brownish, or grey-green, with a dark grey throat and whitish venter ; rarely they have obscure markings on the side of the body and limbs. Females almost always have a bold pattern. A pair of wide, cream-coloured paravertebral stripes may be present from the head to the base of the tail. A row of large, dark brown, cream-edged diamonds may be present down the middle of the back and onto the tail, or a median row of alternating triangular brown spots down the middle of the back may produce a zig-zag pattern. Narrow, cream-coloured, dark brown edged, oblique bands may be present on the sides of the body. A brown crossband may be present on the top of the head, and narrow brown bands may be present on the sides of the head. The tail and limbs may have brown bands. Any one of these markings, or any combination of them, may be

present. Rarely, the female is nearly uniform dark brown, with a few irregular cream-coloured spots. The ventral surfaces are usually yellowish with irregular brownish markings.

REMARKS. The three species described by Spix (1825), listed in the synonymy above, are probably all referable to *Enyalius catenatus*, but the types of these forms have been lost or destroyed. Records in the Zoologisches Staatsammlung des Bayerischen Staates in München indicate that the type of *Lophyrus rhombifer* was present in that museum prior to World War II, but was destroyed during the course of the war. There is no record of the types of the other two species, but it seems probable that they too were originally in München and have also been destroyed. Spix's illustrations show that *margaritaceus* in an adult male, *rhombifer* an adult female, and *albomaxillaris* a juvenile female with colour patterns that are characteristic of several species of *Enyalius* : *catenatus*, *brasiliensis*, *iheringii*, and *boulengeri*. The text descriptions of the species are brief and contain no useful measurements ; however, measurements of the illustrations, if their proportions are to be trusted, indicate that the fourth toe of the adpressed hind limb would extend beyond the tip of the snout in all three forms. Since the adpressed hind limbs of *iheringii* and *boulengeri* fail to reach the tip of the snout these two species may be eliminated as possible synonyms. Those characteristics by which *catenatus* and *brasiliensis* are distinguished from one another cannot be extracted from Spix's description and illustrations, so that the synonymy of Spix's three species with *catenatus* must be considered tentative.

The form described as *Enyalius catenatus paulista* by Ihering (1898 : 102) from São Paulo is said to resemble *catenatus* in the position of the nostril and length of the tibia, but to be intermediate between *catenatus* and *iheringii* in pattern. In view of the extreme variation in pattern in both *catenatus* and *iheringii* it would seem best at present to regard *paulista* as merely a colour variant of *catenatus*.

RANGE. *Enyalius catenatus* occurs in eastern Brazil from the state of Pernambuco in the north at least as far south as the state of Santa Catarina ; a record from Buenos Aires, Argentina seems questionable. A record from an unspecified locality in the state of Goiás indicates that the species may occur some distance inland. Apparently *E. catenatus* overlaps the ranges of all other species of *Enyalius* except *leechii*.

SPECIMENS EXAMINED. *Brazil* : Pernambuco, Iguaraçu B.M.N.H. 88.4.18.5 ; Pernambuco, Recife S.M.F. 60337 ; Pernambuco, no specific locality Z.S.B.S. 934/1920 ; Bahía, near Cabeça do Boi A.M.N.H. 108 (holotype) ; Bahía, no specific locality B.M.N.H. 69.11.3.7, 61.3.23.3, N.M.W. 12954-5, 14075, 18168, Z.S.B.S. 2743/0, S.M.F. 11040 ; Goiás, no specific locality M.C.Z. 4251 ; Rio de Janeiro, Porto Real B.M.N.H. 87.12.29.1-2 ; Rio de Janeiro, Guanabaro, Repressa Rio Grande C.A.S. 96876 ; Rio de Janeiro, Barao Homen de Mello Itatiaya S.M.F. 36217 ; Rio de Janeiro, Petrópolis M.C.Z. 7320 ; Rio de Janeiro, no specific locality M.C.Z. 3717, U.S.N.M. 98603 ; Paraná, Sítio Cafezal, km 92 on São Paulo Rd., Curitiba S.M.F. 64697 ; Santa Catarina, Theresopolis B.M.N.H. 93.9.30.1 ; Espirito Santo, Rio Doce S.M.F. 12511-2 ; no specific locality B.M.N.H. 51.7.17.8., 57.1.11.20, xiii 28b. *Argentina* : Buenos Aires Z.M.H. 10081 (8 exs). *South America* : no specific locality Z.S.B.S. 503/0.

Enyalius iheringii Boulenger

Enyalius iheringii Boulenger, 1885b, p. 192.

SYNTYPES. B.M.N.H. 82.10.4.48-49 from "Rio Grande do Sul", Brazil.

CHARACTERISTICS. (Fig. 5). The dorsal head scales are smooth on the snout, convex and obtusely keeled on the frontal and supraocular regions. The supraoculars are small and numerous laterally, and enlarged medially, the largest equal to or a little smaller than the scales of the supraorbital semicircles. The nasal scale is

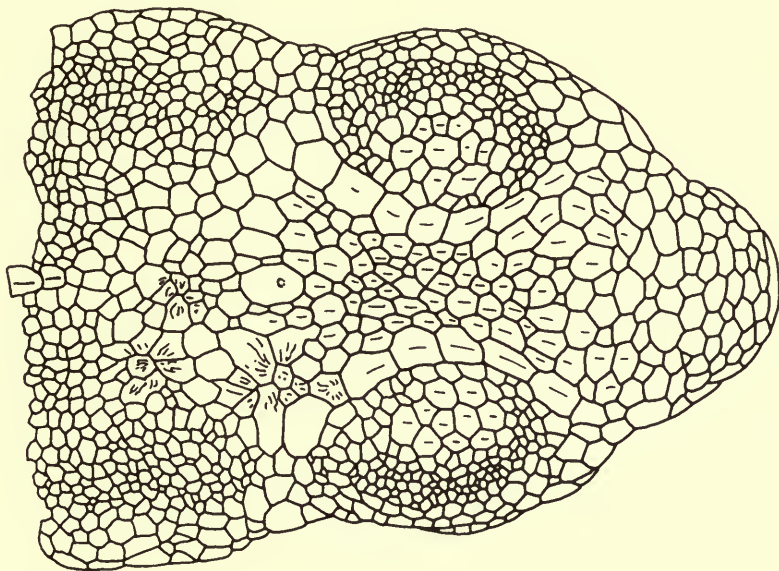


FIG. 5. Dorsal view of the head of *Enyalius iheringii* (B.M.N.H. No. 1946.8.9.4, syntype).

about midway between the tip of the snout and the anterior corner of the orbit. The orbit is bordered in front and below by an arc of about ten large scales, each with a median keel. The temporals are polygonal, juxtaposed, and smooth.

A vertebral row of enlarged scales extends from the occiput to the base of the tail; they are conical on the neck, and arched and keeled along the back. The dorsal scales adjacent to the vertebral row are polygonal, juxtaposed, obtusely keeled, and of various sizes. Laterally they grade into rounded, obtusely keeled, convex scales with more or less triangular granules in the interspaces. The ventral scales are large and distinctly keeled. Scale counts are given in Table 1.

The tail is not autotomic, and the caudal scales are arranged irregularly without a trace of segmentation. Variation in the snout-vent to tail length ratios, and the maximum adult sizes of both sexes are given in Table 2.

The subdigital lamellae are smooth and convex, or may have one or two indistinct keels. The distal four or five lamellae are medially divided. The fourth toe of the adpressed hind limb extends to about the middle of the orbit.

Colour in preservative : males usually are almost uniform brownish or greyish-green above, the throat dark grey, and the belly whitish. Rarely males have indistinct markings similar to the females.

The pattern in females is highly variable, but almost always there is some type of vivid pattern. Often a pair of wide, cream-coloured stripes extend from the paroccipital region of the head to the base of the tail. A middorsal series of large, brown rhombs may be present, or a series of alternating triangles form a zig-zag stripe down the middle of the back. On the sides of the body there may be narrow, oblique light lines, bordered posteriorly by dark brown. The top of the head is sometimes crossed by a dark brown band through the orbits. A light stripe is usually present from the eye to the angle of the mouth. The limbs and feet, and the tail, may have narrow, cream bars. The belly usually is yellowish with faint brownish markings. These markings may exist separately, or in any combination. Rarely a female will be nearly uniform dark brown with a few small, irregular, cream-coloured spots.

RANGE. *Enyalius iheringii* occurs in southeastern Brazil from northern Rio Grande do Sul north to São Paulo. Most of the records for this species are from the state of Santa Catarina. *E. iheringii* apparently occurs within the ranges of *E. catenatus* and *E. brasiliensis*.

SPECIMENS EXAMINED. São Paulo, Osasco A.M.N.H. 74964 ; Santa Catarina, Blumenau N.M.W. 14947, 12958 ; Santa Catarina, New Bremin N.M.W. 12967, S.M.F. 24833, 30303 ; Santa Catarina, Dist. Jaraguá, Rio Itapocú N.M.W. 12964, Z.M.H. 2862 (5 exs) ; Santa Catarina, Joinville N.M.W. 12966 (16 exs), 12961 (17 exs), S.M.F. 11052, Z.M.H. 4536 (7 exs), F.M.N.H. 11622-3, 11388-9 ; Santa Catarina, Theresopolis B.M.N.H. 88.9.21.2-3, S.M.F. 11050, Z.M.H. 2683, N.M.W. 12960 (6 exs) ; Santa Catarina, Hansa B.M.N.H. 1928.11.5.109-113, S.M.F. 24884-9, 11042-8 ; Santa Catarina, Rio Humboldt Z.M.H. 3566 (6 exs) ; Santa Catarina, no specific locality B.M.N.H. 88.4.23.1-2, Z.M.H. 4512 (8 exs), 4536 (7 exs), 1649 (3 exs), U.S.N.M. 40214-5 ; São Paulo, Iguape N.M.W. 12957 ; Rio Grande do Sul, Porto Alegre Z.M.K. 137 ; Rio Grande do Sul, no specific locality N.M.W. 14077, B.M.N.H. 82.10.448-9 [RR 1946.8.9.3-4] (syntypes) ; São Paulo, Santos N.M.W. 12959, 12963 ; Ribeirão Pires Z.S.B.S. 933/1920 ; Taragua N.M.W. 12964 ; no specific locality S.M.F. 11041, Z.M.K. 133-6, 138, U.S.N.M. 58423.

Enyalius brasiliensis (Lesson)

Lophyrus brasiliensis Lesson, 1828, p. 32, pl. 1, fig. 3.

Enyalius rhombifer Duméril & Bibron (part), 1837, p. 231.

SYNTYPES. M.H.N.P. 6816 (2 exs), from " Sainte-Catherine du Brésil ".

CHARACTERISTICS. (Fig. 6). The dorsal head scales are smooth and nearly flat on the snout, convex and keeled in the frontal, prefrontal, and supraocular regions. The supraoculars are small and numerous laterally, and only slightly enlarged medially, the largest about three-fourths as large as the scales of the supraorbital semicircles. The nasal scale is slightly closer to the tip of the snout than it is to the anterior corner of the orbit. The orbit is bordered in front and below by an arc of

nine or ten enlarged scales, each with a median keel. The temporals are polygonal, smooth, and convex.

A vertebral row of enlarged scales extends from the occiput to the base of the tail ; they are conical on the neck, and arched and keeled along the back. The dorsal scales adjacent to the vertebral row are smooth or faintly keeled, polygonal, juxtaposed, and of various sizes. Laterally they grade into rounded, strongly convex scales with more or less triangular scales in the interspaces. The ventral scales are large, distinctly and rather sharply keeled on the chest, less strongly keeled on the belly. Scale counts are given in Table 1.

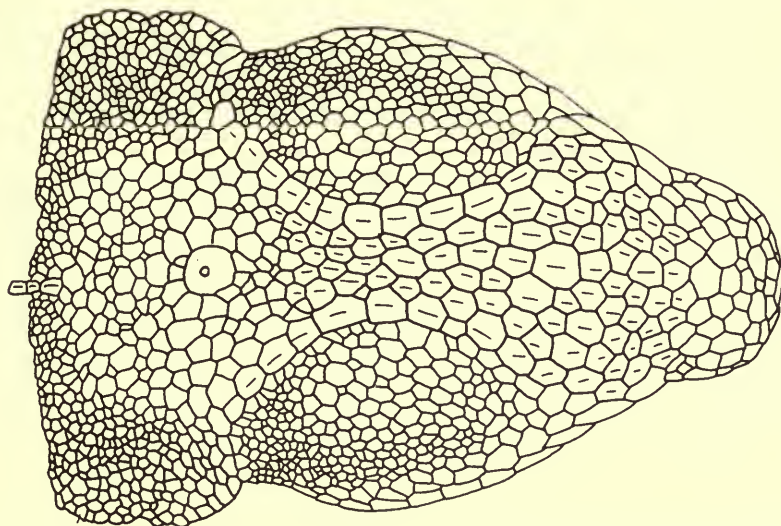


FIG. 6. Dorsal view of the head of *Enyalius brasiliensis* (B.M.N.H. No. 1923.12.4.38).

The tail is autotomic, and the caudal scales are arranged in segments, with five dorsal and three ventral scales in each segment. Variation in the snout-vent length to tail length ratios, and the maximum sizes of both sexes are given in Table 2.

The subdigital lamellae are sharply keeled, usually with three keels on each lamella. A median division of the distal lamellae is absent, or only faintly indicated. The fourth toe of the adpressed hind limb extends beyond the tip of the snout.

Colour in preservative : females are dark, chestnut brown above, with a pair of wide, cream-coloured paravertebral stripes and/or a series of rather large, dark brown diamonds edged in cream down the middle of the back. A darker brown band crosses the top of the head through the orbits, and another extends from the eye to the posterior upper labials, and another extends back on the temporal region from the eye through the tympanum, thence widening on the side of the neck. The upper surfaces of the limbs have short, brown bands. The tail is indistinctly banded. Ventral surfaces of the body and limbs are yellowish, rather heavily marked with small, irregular brown spots.

Males are dark purplish-grey above, the venter is dirty white, the gular region dark grey, and the ventral surfaces of the limbs have indistinct darker markings.

REMARKS. The description of *Lophyrus brasiliensis* is brief and includes no information that would permit one to definitely assign it to the genus *Enyalius*. The illustration (Lesson, 1828 : pl. 1, fig. 3) is that of a rather slender, long-tailed lizard, dark purple above, light blue below, with bold, white spots on the chin and belly. The syntypes, although not listed by Guibé (1959), still exist in the Paris Museum. The larger of the two appears to be the specimen illustrated by Lesson : the supraocular region on the left side is mashed down in a peculiar way that is reproduced exactly in the illustration.

Duméril & Bibron (1837 : 231) listed *Lophyrus brasiliensis* as a synonym of *Enyalius rhombifer* Spix. Their characterization of the latter is based on three specimens, all of which have keeled subdigital lamellae. Two of the specimens (M.H.N.P. No. 2373 and 6815) are from Cayenne, and are of another species. The third, No. 6814, is a specimen of *E. brasiliensis*.

RANGE. All specific localities for *Enyalius brasiliensis* are from southeastern Brazil and northeastern Uruguay, from Montevideo in the south to Rio de Janeiro in the north. *E. catenatus* and *E. iheringii* occur within the range of *E. brasiliensis* (Fig. 10).

SPECIMENS EXAMINED. *Brazil* : Santa Caterina, no specific locality M.H.N.P. 6816 (2 exs) (syntypes) ; Rio de Janeiro, Massif de Tijuca, Serra dos Orgãos M.H.N.P. 02.368 ; Rio de Janeiro, Mangaratiba A.M.N.H. 62143 ; Rio de Janeiro, no specific locality M.H.N.P. 1918.25, B.M.N.H. 74.5.21.5 no specific locality B.M.N.H. xxiii.28c. *Uruguay* : Montevideo B.M.N.H. 1923.12.14.38.

Enyalius boulengeri sp. nov.

Enyalius rhombifer (part) Duméril & Bibron, 1837, p. 231.

HOLOTYPE. Z.M.H. No. 1338. An adult female from the state of Espírito Santo, Brazil; one of a series of 15 specimens with the same data as the holotype received from a Mr. Michaelis on May 3, 1898.

DIAGNOSIS. *E. boulengeri* differs from *E. bilineatus*, *E. pictus*, *E. bibronii*, and *E. iheringii* in having distinctly keeled subdigital lamellae, and the distal lamellae not medially divided. Compared with those species of *Enyalius* with keeled subdigital lamellae, *E. boulengeri* differs from *E. brasiliensis* in having fewer vertebral scales and fewer midbody scales (see Table I), a shorter tail (see Table II), and shorter hind limbs, and differs from *E. leechii* in having smaller supraoculars, shorter hind limbs, less distinctly keeled head scales, and, possibly, in having a vertebral crest.

DESCRIPTION OF THE HOLOTYPE. (Fig. 7). The dorsal head scales are convex, especially in the frontonasal region, and keeled in the supraocular and parietal regions. The supraoculars are small laterally, becoming only slightly enlarged medially ; the largest supraoculars are about one-third as large as the largest scales of the supraorbital semicircles. The nasal scale is about equal distance between the tip of the snout and the anterior corner of the orbit. The orbit is bordered below by

an arc of eight enlarged scales, each with a median keel. The temporals are strongly convex and weakly keeled.

A vertebral row of enlarged scales extends from the occiput to the base of the tail; they are conical on the neck, and arched and keeled along the back. There are 32 vertebral scales counted from the occiput to a line even with the anterior margins of the thighs held at right angles to the trunk.

The dorsal scales adjacent to the vertebral row are polygonal, juxtaposed, faintly and obtusely keeled, and of various sizes. Laterally they grade into smaller,

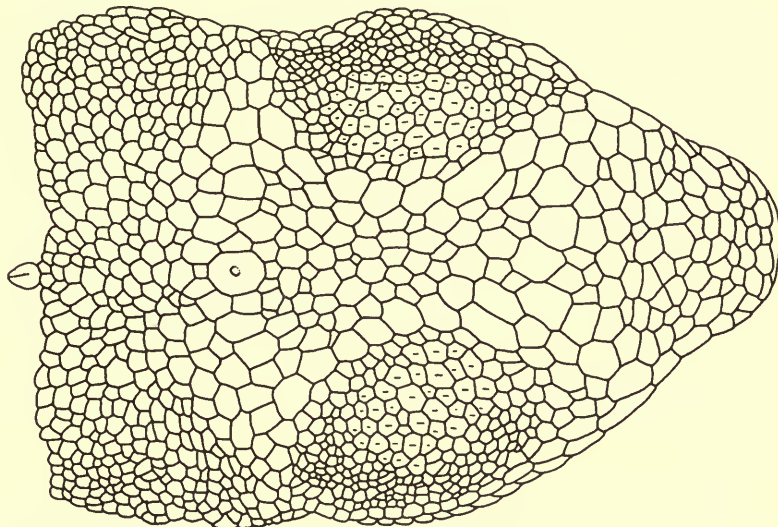


FIG. 7. Dorsal view of the head of *Enyalius boulengeri* (Z.M.H. No. 1338, holotype).

rounded, convex scales with more or less triangular granules in the interspaces. The ventral scales are about three times as large as the dorsals, subimbricate, and distinctly keeled. There are 126 paravertebral scales counted as are the vertebral scales, and 136 scales around the middle of the body midway between the limb insertions.

The tail is autotomic, and the caudal scales are arranged in segments, with five dorsal and three ventral scales in each segment. The snout-vent length is 108.6 mm., the tail length 183.0 mm.

The subdigital lamellae have three or four sharp keels. The distal lamellae of each toe are not divided medially. The fourth toe of the adpressed hind limb extends to the anterior margin of the orbit.

The head is uniform dark brown above and on the sides. Down the middle of the back is a wide, zig-zag stripe of dark brown, formed by alternating triangles. Flanking the median zig-zag on each side is a wide paravertebral stripe of creamy yellow, flecked with brown, extending from just behind and above the tympanum to the base of the tail. The sides of the neck and body below the light paravertebral stripes are dark brown with indistinct lighter markings. The upper surfaces of the limbs are dark brown with irregular yellowish spots. The ventral surface of the

body and limbs is light yellowish-tan with scattered small, brown spots ; the throat is slightly darker than the belly. The tail is yellowish-tan with irregular brown spots.

VARIATION. A total of 48 have been examined. Of these, 22 females and 7 males are sufficiently well preserved to provide accurate scale counts and measurements. The maximum snout-vent lengths in both sexes, and variation in the snout-vent length to tail length ratios are given in Table 2. Variation in the vertebral, paravertebral, and midbody scale counts are given in Table 1.

The colour pattern is highly variable. Females have a pair of wide, creamy-yellow paravertebral stripes, a median series of large, dark brown rhombs or a series of alternating brown triangles that form a zig-zag vertebral stripe as in the holotype. The tail and limbs may have creamy-yellow bands or spots, and the belly is yellowish-tan, and often rather heavily marked with irregular brown spots. In about one-half of the females examined the paravertebral stripes and/or median rhombs are restricted to, or are most intense on, the neck and shoulders. The males may be uniform greyish-green or brown, but more often have a pattern similar to, but less vivid than, the females.

REMARKS. Duméril & Bibron (1837 : 231) referred three specimens to *Enyalius rhombifer* Spix, two of which (M.H.N.P. 2373 and 6815) were said to come from Cayenne (French Guiana), and which belong to the species described here as *boulengeri*. As indicated earlier in this paper *E. rhombifer* is very probably a synonym of *E. catenatus* or *E. brasiliensis*, but definitely not the same as that species described here as *boulengeri*.

RANGE. Records of *Enyalius boulengeri* are from Espirito Santo and adjacent southeastern Minas Geras, Brazil (Fig. 10). Two specimens in the Paris Museum are said to come from French Guiana, but this record seems doubtful. *E. boulengeri* probably occurs within the ranges of *E. catenatus*, *E. bilineatus* and *E. bibronii*, and possibly *E. pictus*.

PARATYPES. *Brazil* : Espirito Santo, Chaves M.C.Z. 79025 ; Espirito Santo, no specific locality Z.M.H. 1338 (holotype), 2217 (14 exs), N.M.W. 12956 (13 exs) ; between Minas Gerais and Espirito Santo Z.M.H. 2205 (15 exs) ; Minas Gerais, Santa Leopoldina Z.M.H. 2546 (2 exs). *Cayenne* (possibly in error) : no specific locality M.H.N.P. 2373, 6815.

Enyalius leechii (Boulenger)

Enyalioides leechii Boulenger, 1885b, p. 473.

HOLOTYPE. B.M.N.H. 86.10.14.1 [RR 1946.8.9.7], from " Santarem ", Brazil.

CHARACTERISTICS. (Fig. 8). The dorsal head scales anterior to the parietal region are distinctly uncarinate ; those posterior to the parietal region and in the temporal region are smooth and convex. The supraoculars are small and numerous peripherally, enlarged centrally, the largest a little smaller than the scales of the supraorbital semicircles. The distance between the nasal scale and the tip of the snout is a little less than one-half the distance between the nasal and the anterior

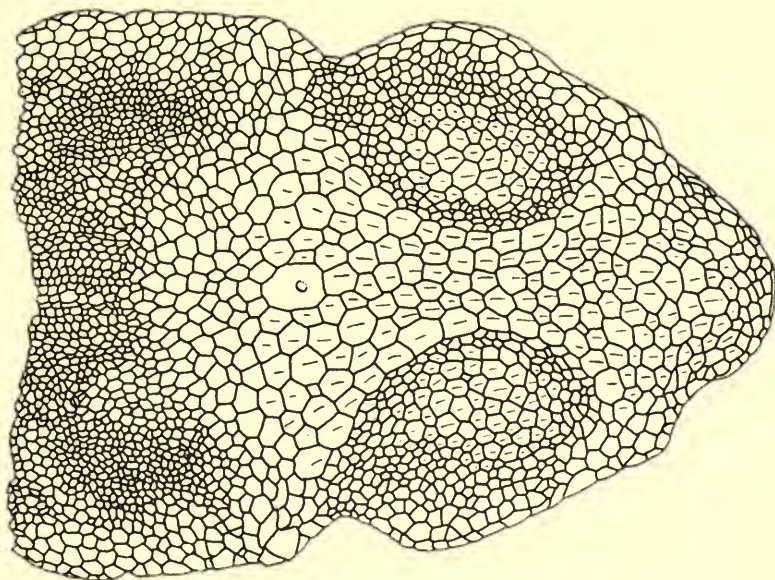


FIG. 8. Dorsal view of the head of *Enyalius leechii* (B.M.N.H. No. 1946.8.9.7, holotype).

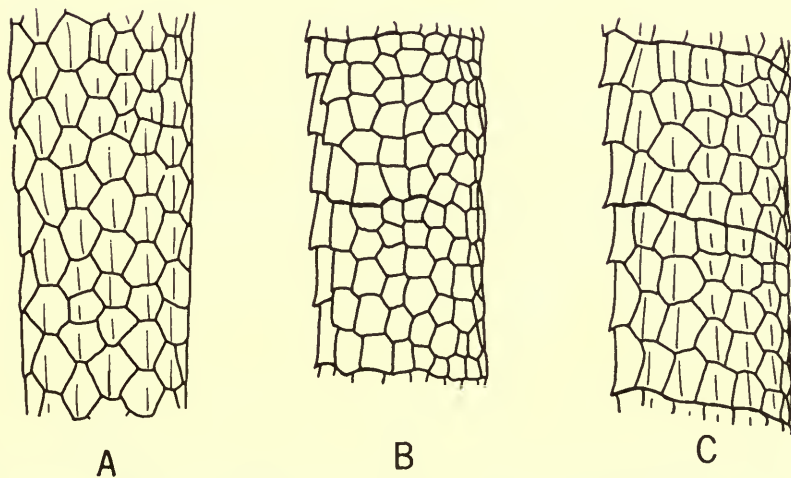


FIG. 9. Lateral view of the midsection of the tail of *Enyalius bilineatus* (A), *E. pictus* (B), and *E. bibronii* (C).

corner of the orbit. The orbit is bordered in front and below by an arc of 14 scales, each of them arched and with a median keel. The temporals are polygonal, juxtaposed, and convex.

Along the middle of the back is a discontinuous vertebral row of scales that are scarcely larger than the adjacent scales, and which do not form a crest or serration. The dorsal scales adjacent to those along the midline are polygonal, juxtaposed, convex, obtusely keeled, and of various sizes. Laterally these grade into smaller, more or less triangular granules in the interspaces. The ventral scales are large and distinctly keeled. Scale counts are given in Table 1.

The tail is autotomic, and the caudal scales are arranged in segments with five dorsal and three ventral scales in each segment. The snout-vent to tail length ratio, and the size of the unique type are given in Table 2.

The subdigital lamellae have three sharp keels that end in a short spine. The fourth toe of the adpressed hind limb extends just beyond the tip of the snout.

Colour in preservative : the head and body are chestnut-brown above. A faint, thin, dark line extends from the eye to the angle of the jaw, then back along the lower border of the ear to the insertion of the forelimb, effecting a sharp demarcation between the darker colour of the side of the neck and the lighter colour of the throat and chin. A wide, yellowish stripe on each side of the neck ends abruptly at the shoulder. A yellowish-brown diamond is present on each shoulder between the paravertebral stripes. The tail has a dorsal and a ventral series of brown, cream-edged ovals, some of which are confluent on the sides. The limbs have indistinct dark crossbands. The venter is yellowish, unmarked except for a pair of oblique brown lines on the throat. As yet no males are known for this species.

REMARKS. Although Boulenger (1885b : 473) placed this species in *Enyalioides*, it has none of the distinguishing characteristics of that genus, but has all of the generic characteristics of *Enyalius* (see following discussion and comparison of *Enyalius* and *Enyalioides*). Its most peculiar feature is the absence of a vertebral crest, present in all other species of *Enyalius*, as well as in *Enyalioides*. In the type description Boulenger suggested that the absence of a crest in this specimen may be anomalous. Even if a crest is normally present, *leechii* is sufficiently distinct in other characters to be recognized as a valid species.

RANGE. *Enyalius leechii* is known only from the type locality : Santarem, on the Rio Amazon, state of Pará, Brazil (Fig. 10). This locality is far removed from the known records of all other species of *Enyalius*.

SPECIMENS EXAMINED. Brazil : Pará, Santarem B.M.N.H. 85.10.14.1 [RR 1946.8.9.7] (holotype).

A KEY TO THE SPECIES OF *ENYALIUS*

- | | | |
|---|--|----------------|
| 1 | All subdigital lamellae smooth, or some of them with one or two indistinct keels ; the distal 4 or 5 lamellae of each digit with a median, longitudinal groove | 4 |
| - | All subdigital lamellae distinctly keeled ; the distal 4 or 5 lamellae without a median groove, or the groove obscured by the keels | 2 |
| 2 | Dorsal head scales, including those on the snout, distinctly keeled ; vertebral crest absent? | <i>leechii</i> |
| - | Scales on the snout smooth, other dorsal head scales smooth or keeled ; vertebral | |

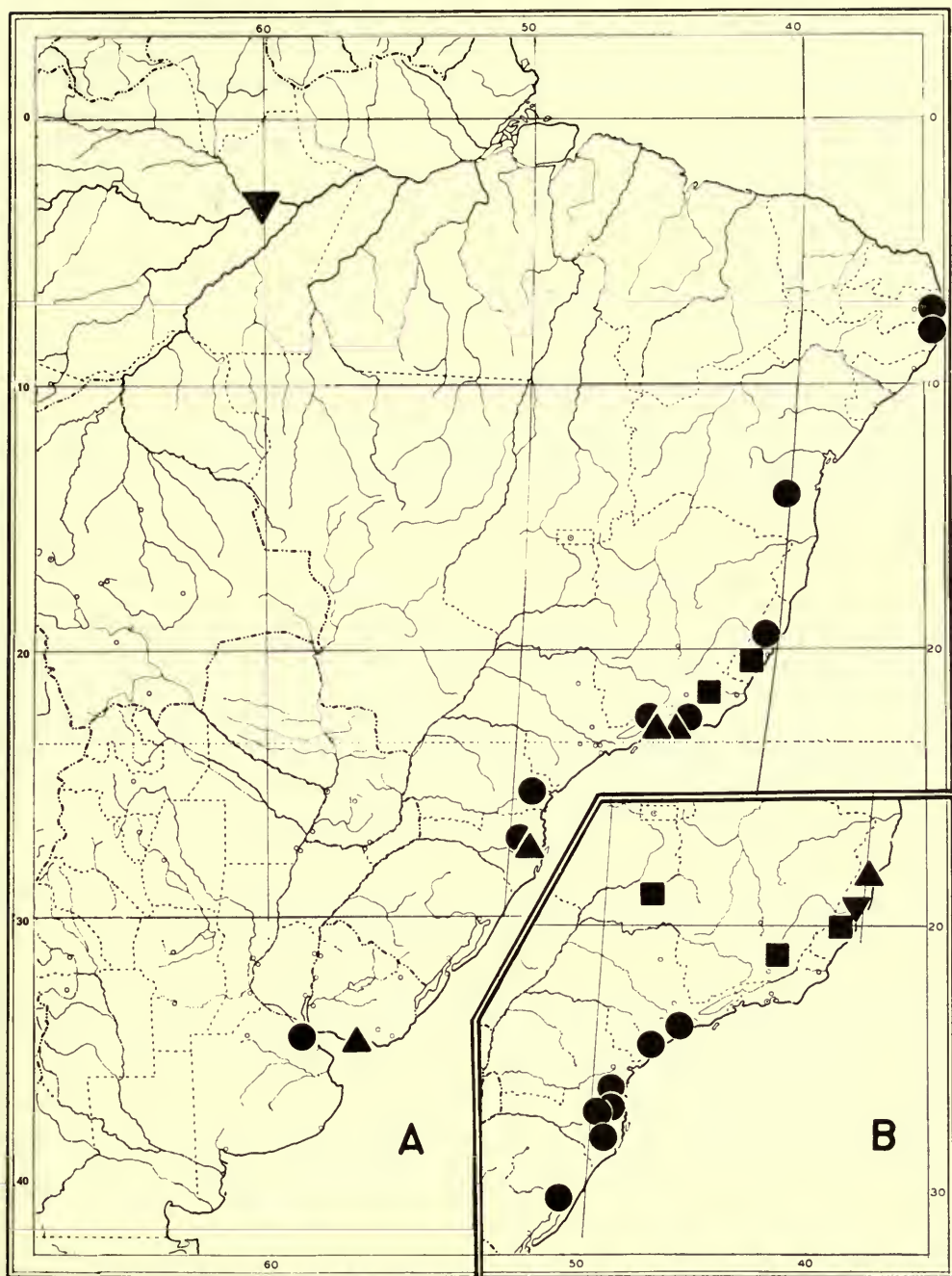


FIG. 10. Maps of eastern South America showing localities for *Enyalius* : A. *E. calenatus* (circles), *E. boulengeri* (squares), *E. brasiliensis* (triangles), and *E. leechii* (inverted triangle) ; B. *E. bilineatus* (squares), *E. iheringii* (circles), *E. bibronii* (triangles), and *E. pictus* (inverted triangle).

	crest present	3
3	Tail not more than 1.92 times snout-vent length ; adpressed hind limb extends to between orbit and tip of snout	<i>boulengeri</i>
-	Tail at least 2.04 times snout-vent length ; adpressed hind limb extends beyond tip of snout	<i>brasiliensis</i>
4	Tail more than 2.5 times snout-vent length ; usually an elongate subocular ; belly with three longitudinal dark stripes	<i>bilineatus</i>
-	Tail less than 2.5 times snout-vent length ; no elongate subocular ; no longitudinal stripes on belly	5
5	Ventral scales smooth	6
-	Ventral scales keeled	7
6	Tail more than twice as long as head and body ; not more than 60 scales in vertebral crest between occiput and anterior margin of thigh ; both sexes marked with wide crossbands	<i>pictus</i>
-	Tail less than twice as long as head and body ; more than 60 scales in vertebral crest ; females not with wide crossbands (males unknown)	<i>bibronii</i>
7	Tail not autotomic, caudal scales not in regular segments ; adpressed hind limb reaches about to middle of orbit	<i>iheringii</i>
-	Tail autotomic, caudal scales in regular segments with 5 or 6 dorsal and 3 ventral scales per segment ; adpressed hind limb reaches beyond tip of snout	<i>catenatus</i>

Enyalius compared with *Enyalioides*

During the last century a group of species that are quite different from those referred here to *Enyalius* was included in that genus until Boulenger (1885b : 112) set them apart in a new genus, *Enyalioides*. Although the two genera are morphologically very distinct, and do not overlap geographically, some confusion between them has remained. Boulenger listed the characteristics of the genera, excluding those that are common to both, as follows:

<i>Enyalius</i>	<i>Enyalioides</i>
a. Body feebly compressed	Body compressed
b. A slight dorsonuchal crest	A dorsal crest
c. No gular pouch	A more or less developed gular sac in males
d. Digits scarcely compressed, not denticulate laterally, with smooth or obtusely keeled lamellae inferiorly	Digits compressed, with sharply keeled lamellae inferiorly
e. No femoral pores	Males with a few femoral pores (? except in <i>palpebralis</i>)
f. Tail rounded or slightly compressed	Tail compressed

In addition to proposing the genus *Enyalioides*, Boulenger (1885b : 473) in the same work described a new species, *Enyalioides leechii*. Apparently he considered sharply keeled subdigital lamellae to be the most significant character distinguishing *Enyalioides* from *Enyalius*, for *leechii*, which has keeled lamellae, corresponds in all

other characteristics listed above with *Enyalius*. Gans & Vanzolini (1954), in suggesting the synonymy of *Enyalius coerulescens* (Cope, 1876 : 169) with *Enyalioides laticeps* (Guichenot, 1855 : 20), also stressed the presence of keeled lamellae in the type of *coerulescens*.

Enyalius and *Enyalioides* are unquestionably distinct, and probably not very closely related genera. There are several major osteological differences, and numerous external differences between them. The keeling of the subdigital lamellae,

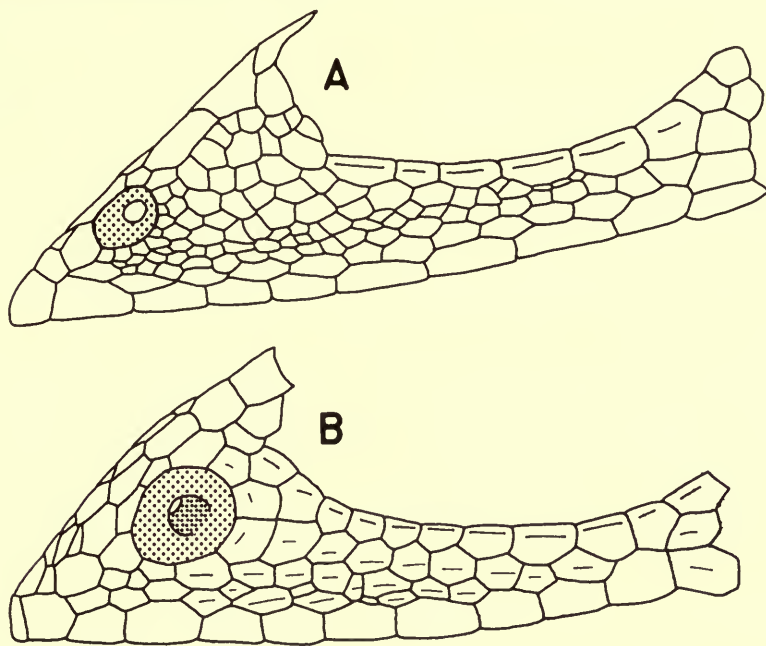


FIG. 11. Left lateral view of the snout region of *Enyalius catenatus* (A), and *Enyalioides praestabilis* (B). The nasal scale is stippled.

however, is not one of them. The lamellae are sharply keeled in three species of *Enyalius*, smooth or obtusely keeled in one, and smooth in four others. *Enyalioides* is badly in need of revision at the species and subspecies level, but there is a number of characters which all individuals of the genus have in common, as opposed to *Enyalius*. The two genera may be compared as follows : (data on *Enyalioides* based on examination of all forms, including types of *heterolepis*, *mocquardi*, *festae*, *laticeps*, *planiceps*, *microlepis*, *palpebralis*, and *praestabilis*).

Enyalius

- a. Nasal scale small, its diameter about one-fifth the distance between orbit and tip of snout ; convex, with the

Enyalioides

- Nasal scale very large, its diameter almost one-third the distance from orbit to tip of snout ; convex in front of

Enyalius

nostril directed laterally ; 4 or 5 scales between nasal and anterior corner of orbit (Fig. 11).

- b. Dorsal head scales smooth, or with a low keel.
- c. Superciliary ridge less strongly projecting; anterior superciliaries elongate, with oblique sutures.
- d. Subdigital lamellae on hind foot not forming a comb.
- e. Tail feebly compressed at base, slender and rounded for most of its length.
- f. Vertebral crest ends near base of tail, no double crest on tail. Segmental arrangements of caudals (in species with autotomy) not readily apparent.
- g. Dorsal body scales polygonal, juxtaposed, smooth or keeled.
- h. Males without femoral pores.
- i. No gular pouch in males. Throat usually darker but not with an area of intense black.

Enyalioides

nostril, concave behind, with nostril directed posterolaterally ; 1 or 2 scales between nasal and anterior corner of orbit (Fig. 11).

- Dorsal head scales compressed, and raised to a high keel, or pyramidal, with several keels.
- Superciliary ridge strongly projecting; the anterior superciliary scales not elongate, with vertical sutures.
- Subdigital lamellae on hind foot form a distinct comb.
- Tail strongly compressed for most of its length.
- A double crest most of the length of the tail. Segmental arrangement of caudals very apparent due to marked anterior-posterior increase in scale size within each segment.
- Dorsal scales of body variable, homogenous or heterogenous, smooth or keeled, imbricate or juxtaposed, but not as in *Enyalius*.
- Femoral pores present or absent in males and/or females.
- Males with a well developed gular pouch, usually associated with a region of intense black on the throat.

Enyalius compared with *Anisolepis* and *Aptycholaemus*

In his description of *Anisolepis* Boulenger (1885c : 86-7) stated that it is " allied to *Enyalius*, *Urostrophus*, and *Liosaurus*, which have likewise smooth infradigital lamellae, no femoral pores, and, like *Polychrus* and the Geckonidae, abdominal ribs and no fontanelle in the sternum ". Later, in his description of *Aptycholaemus* (Boulenger, 1891 : 85), he stated that this genus is " allied to *Urostrophus*, D. & B., and *Anisolepis* Blgr., but differs from both in the absence of a gular fold and in dorsal

lepidosis". *Anisolepis* and *Aptycholaemus* are indeed very similar to each other, and of iguanids are most like *Enyalius*.

Anisolepis, *Aptycholaemus*, and *Enyalius* are very similar osteologically, and have in common the following external features: supraorbital semicircles medially separated; juxtaposed, polygonal head scales; a small but distinct interparietal scale; a small, convex nasal scale placed laterally below the canthal ridge; several elongate, overlapping anterior superciliary scales; dorsal body scales of various sizes and not evenly aligned in rows; small, juxtaposed lateral body scales; large ventral scales; granular postfemoral and posterior suprafemoral scales; no femoral pores; a long, slender, rounded tail.

The differences that separate *Anisolepis* and *Aptycholaemus*, considering the two together, from *Enyalius* are few and relatively trivial: they have no vertebral scale row, their distal subdigital lamellae, which are smooth, do not have a median groove, and their hind limbs are shorter, when adpressed reaching no farther than the ear. *Aptycholaemus* further differs from *Enyalius* in having no transverse gular fold, and a very small ear opening. *Anisolepis* further differs from *Enyalius* in its exceedingly long tail, well over three times the length of the head and body.

Enyalius bilineatus is in some respects transitional between *Anisolepis* and *Aptycholaemus* on the one hand, and the remaining species of *Enyalius* on the other. It is the only form with an elongate subocular scale as in *Anisolepis* and *Aptycholaemus*. Although a vertebral scale row is present in *E. bilineatus* it forms at most a low serration rather than a distinct denticulation. The keels of its ventral scales form distinct parallel lines as in *Anisolepis* and *Aptycholaemus*. Also, as in these two genera, as well as in some other species of *Enyalius*, the tail is not autotomic, its subdigital lamellae are smooth, and there is no sexual dichromatism.

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THE GENUS GEONEMERTES



C. F. A. PANTIN
WITH AN APPENDIX BY
JANET MOORE

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BY

CARL FREDERICK ABEL PANTIN

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Pp. 261-310; Frontispiece, 28 Text-figures

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Two New Zealand species of *Geonemertes* for comparison; above, *G. pantini*;
below, *G. novaezealandiae*.

Photograph by Elizabeth J. Batham



THE GENUS GEONEMERTES

By C. F. A. PANTIN

FOREWORD

Among the late Professor C. F. A. Pantin's¹ papers was a manuscript "The Genus *Geonemertes*", written in 1952 but never published because of the influx of new material. At the invitation of Mrs. A. M. Pantin and Dr. J. E. Smith (Professor Pantin's scientific executor) Dr. Janet Moore has prepared the original manuscript for press by writing an appendix compiled from Professor Pantin's notes and correspondence (1952-66). The original manuscript required only very minor editing, and the appendix consists as far as possible of quotations from Professor Pantin's letters. There are, however, a few original observations and comments on the material. These are indicated in square brackets and initialled. The appendix also records the localities where various species have been found, and indicates the stage reached in various unfinished lines of research on which the account is based.

In putting this account together Dr. Moore has studied and become thoroughly familiar with the microscopic slides and specimens left by Professor Pantin and it is hoped that she will now continue the investigations where he left off. The slides and specimens are to be deposited in the British Museum (Natural History).

The illustrations have been drawn by Mr. W. B. Amos and are mostly based on sections selected and roughly sketched by Professor Pantin.

J. P. HARDING
Keeper of Zoology

THE GENUS

IN 1937 Waterston and Quick recorded the occurrence of the terrestrial nemertine *Geonemertes dendyi* Dakin in South Wales. The subsequent discovery of many specimens in South Devon (Pantin, 1944) enabled me to make a study of this interesting organism; a study which led to a consideration of the relationship of the species of the genus. This is of peculiar interest, because it concerns the one terrestrial genus of an almost exclusively marine phylum, and because several of the species occur in isolation on oceanic islands. It is this relationship of the species which we shall now discuss.

The characters of the genus have been summarized by Hett (1927), Brinkmann

¹ Professor Pantin, who died on 14th January, 1967, was at that time Chairman of the Trustees of the British Museum (Natural History).

(1947) and others. Inspection at once shows that the majority of these are no more than generalized metanemertine characters, particularly those of the relatively unspecialized families of the Tetrastemmatidae and Prosorhochmidae. Such characters are the single stylet, coincidence of mouth and rhynchostome, anteriorly-directed midgut caecum and the anterior diverticula of the intestine, the cerebral sense-organ. The only other common characters of all the described species are

1. adaptation to terrestrial existence ;
2. the degenerate state of the head furrows (Kopffürchen) ;
3. the extensive development of the excretory system throughout the length of the body : for though the existence of such a system has been denied in many species it will be shown below that careful search always reveals its presence.

The first of these characters cannot of itself suffice to distinguish a genus without begging the question that it is not of polyphyletic origin ; a possibility which must be considered in view of the extraordinary distribution of the genus, and one which has been suggested more than once (Bürger, 1895 ; Brinkmann, 1947). The second and third characters might, as defined above, be no more than natural concomitants of adaptation to land life even if this took place several times independently : this is particularly the case since reduction of the head-furrows and development of the excretory systems have taken place on different lines in different species.

It is therefore necessary to consider the relationships of the species of the genus afresh. As Brinkmann (1947) points out, this is difficult because of the inadequate description of many of the species. He points out in particular how slender is our knowledge of the vascular and excretory systems, and suggests that these should not be employed in characterizing species because of the difficulty of observing them. Were this objection valid it would be very serious, for it is in just these systems that we may look for extensive and various adaptations to terrestrial conditions. Fortunately there is no doubt that when sections are cut in an appropriate plane (tangential to the surface) and stained with polychrome stains such as Mallory's triple stain, the major features of both these systems are easily seen even in indifferently fixed material. In the present work particular attention has been paid to these systems, and, in conjunction with other characters, they supply ample evidence to define the relations of many of the species of the supposed genus.

By good fortune I have been able to examine a number of the known species and thereby to add some significant facts about them. My survey has been based upon specimens and slides of *Geonemertes australiensis* Dendy in the collection of the late Professor Dendy at King's College, London : of *G. australiensis* Dendy, *G. hillii* Hett and *G. pelaensis* Semper¹ in the collection of Miss M. Hett : of *G. paelansis* Semper in the collection of Dr. Wesley Coe : of *G. rodericana* Gulliver from the British Museum : of *G. arboricola* Punnett from the Zoological Museum, Cambridge : of a specimen of *G. nightingaleensis* Brinkmann collected from Nightingale Island by the Norwegian Scientific Expedition 1937-38 : of specimens of *G. agricola* Willemoes-Suhm kindly collected for me by Dr. Brian Boden during the summer of 1951 in Bermuda : and of an undescribed specimen from Ceylon in the Cambridge Museum.

¹ This is often misnamed *palaensis* Semper.

These have been compared with specimens of *G. dendyi* collected by myself and, where necessary, with the freshwater *Prostoma graecense* (Böhmig) obtained from the River Cam (Braithwaite and Clayton, 1945), and with specimens of *Prosorhochmus clapedii* Keferstein from crevices near high water mark at Wembury and the Yealm, Plymouth. Professor Dendy's slides of *G. australiensis* were those on which his paper (1892) was based and his slides of *G. novaezealandiae* (Dendy, 1894, 1895) were restained and examined: Miss Hett's slides were those on which her papers on *G. hillii* and *G. pelaensis* were based (1924, 1927), and Dr. Wesley Coe's slides were those of his 1940 paper.

For reasons which will become apparent it is convenient to discuss first the Australian species, then those which I find to be related to *G. pelaensis*, and then to discuss the relation of the remaining species to these two groups.

The characters of the species

The relationship of species is determined by the number and by the quality of the

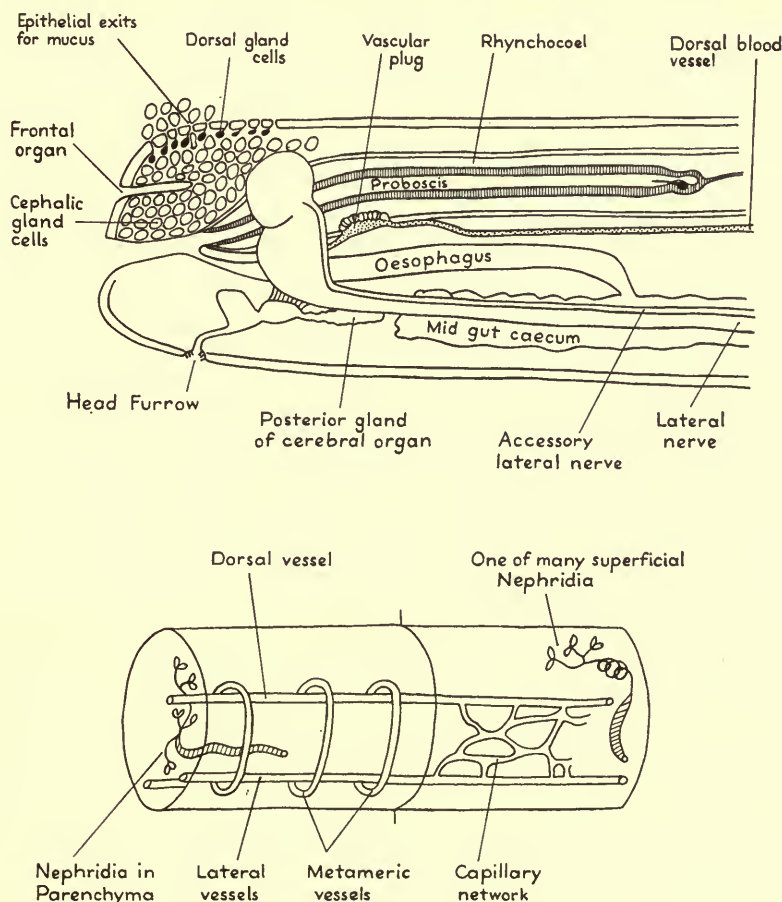


FIG. 1. Anatomical scheme illustrating various geonemertine characters.

characters they possess in common. It is necessary therefore to appreciate the nature of the characters concerned. Some of the special characters upon which the argument of this paper turns are illustrated by Figure 1. The figure is diagrammatic and no one species possesses all the characters represented in it. Its sole, though important, purpose is to clarify the terminology used.

THE AUSTRALIAN GROUP

Let us first consider the species *G. dendyi*, *G. australiensis* and *G. hillii*. Dakin (1915) and Stammer (1934) have given incomplete accounts of *G. dendyi*, but the descriptions of the other two species by Dendy (1892) and Hett (1924) are fairly complete. My own observations have confirmed much of these descriptions and have added some new facts, particularly in *G. dendyi*.

In addition to their generalized metanemertine features the three species possess many special characters in common :

1. There is excessive multiplication of the four primitive metanemertine eyes over the rounded head—almost to an “ommatidial” condition with about twenty, forty and eighty eyes distributed over the head in the three species respectively.
2. The frontal organ, commonly present in nemertines, is absent in these species. This organ is a median anteriorly placed canal which in most nemertines receives the secretion of the cephalic glands (Fig. 1). In the three species we are discussing the secretion of these glands seems to escape to the exterior by extemporized channels through the basement membrane and epithelium of the head, as Dendy suggests in *G. australiensis*. I find this is true in *G. dendyi* (Figs. 9, 10) and re-examination of the slides of *G. hillii* shows the same thing.
3. “Dorsal gland cells” as described by Dendy (1892) and Hett (1924) are present. These seem to be integumentary glandular cells sunk below the muscle layer of the anterodorsal surface. They have a strong affinity for borax carmine and for orange G. in Mallory’s triple stain (Fig. 9).
4. Arising from the dorsal lobe of the brain and running along the dorsal surface of the lateral nerve on each side is an “accessory lateral nerve”; a structure only found elsewhere in the genus *Oerstedia*, in the pelagic Polystilifera and some southern Tetrastemmatidae (Stiasny-Wijnhoff, 1930) such as *Tetrastemma gulliveri* (Bürger, 1893) (Fig. 2).
5. In *G. australiensis* and *G. dendyi* the cerebral organs are of similar structure and possess a large posterior glandular extension corresponding to the “oesophageal organ” of Dendy (Dendy, 1892) (Fig. 13). The duct from each cerebral organ runs forward and opens ventrally. Hett (1924), who compared the anatomy of *G. hillii* and *G. australiensis*, made no note of any difference in the structure of their cerebral organs and made no comment. My comparison of the original slides of both these species with sections of *G. dendyi* confirms the essential similarity of the whole cerebral organ in all three. Minor differences will be noted later.

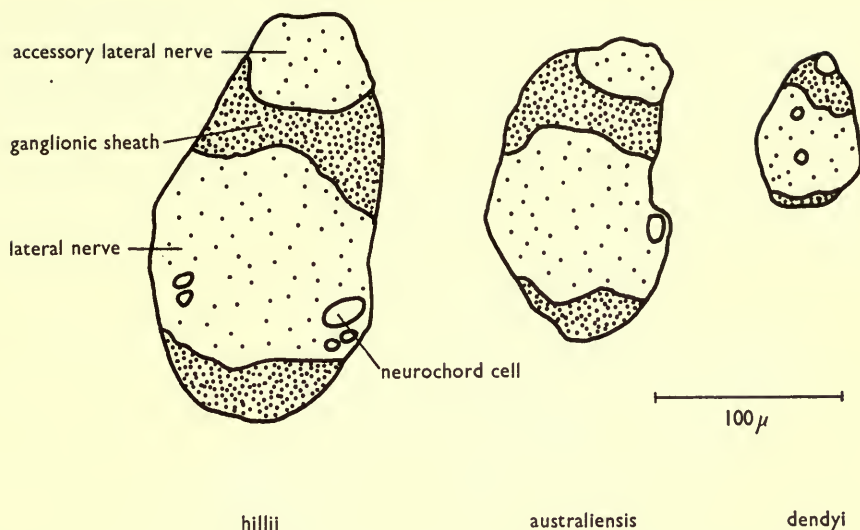


FIG. 2. Camera lucida drawings of the lateral nerve in the three Australian species of *Geonemertes*, just in front of anterior gut diverticula, to show the relative sizes of the accessory lateral nerve.

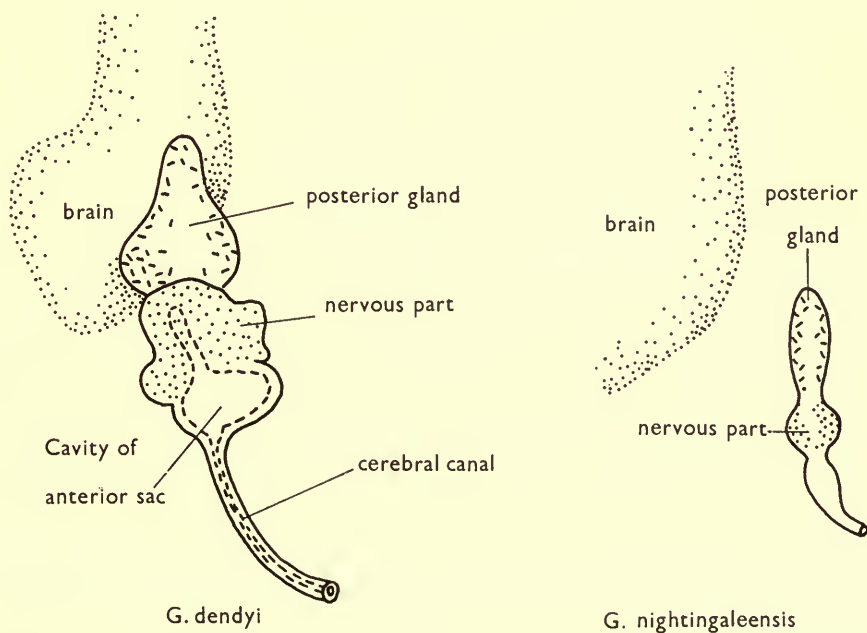
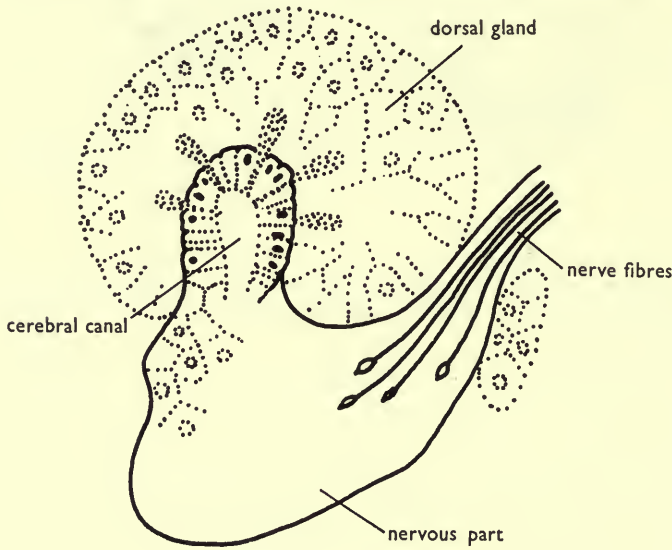


FIG. 3. Cerebral Organs of *G. dendyi* and *G. nightingaleensis* in longitudinal section.

6. For most of its course the dorsal blood-vessel of metanemertines runs above the gut and just below the rhynchocoel, but in the neighbourhood of the oesophagus it enters the rhynchocoel and runs along the ventral wall till it leaves the rhynchocoel near the point where the dorsal vessel divides from the cephalic loop. In *G. australiensis* (Dendy, 1892) the dorsal blood-vessel pierces the rhynchocoelic sheath but remains outside the rhynchocoelic cavity. Just behind the ventral cerebral commissure the vessel divides, and its branches supply two curious plugs of tissue which alone separate the blood from the



G. pelaensis

FIG. 4. Cerebral Organ of *G. pelaensis* in transverse section.

rhynchocoel. I have found precisely similar paired structures in *G. dendyi* supplied by anterior bifurcation of the dorsal vessel (Figs. 14, 15, 16). Hett (1924) notes only one such plug in *G. hillii* with certainty. Re-examination of her sections shows that here also there are two independent and well-developed plugs. (Owing to slight obliquity of the sections the left-hand plug is in slide "Nem. J.P.H. D6" and the right-hand one in slide "Nem. J.P.H. D7".) Some other nemertines possess rhynchocoelic vascular tissue plugs in the dorsal vessel, but, as in *Prostoma graecense* (see Böhmig, 1898) and in *Prosorhochmus clapedii*, there is only one such plug (Fig. 23, T.S. *Prosorhochmus*).

7. The lateral blood-vessels supply an anastomosing subdermal network of capillary blood-vessels, not the usual quasi-metameric arches of the metanemertine (Fig. 7).
8. The nephridia in *G. dendyi* and *G. hillii* consist of numerous flame-cells, typically in pairs, situated immediately below the dermal muscle-layer, like

the capillary blood-network. Each flame-cell has a single nucleus at its head, and connects with end canals which join to convoluted common canals, which pass abruptly into second convoluted canals with thick walls of radially organized cytoplasm, and each of which finally empties to the exterior by one

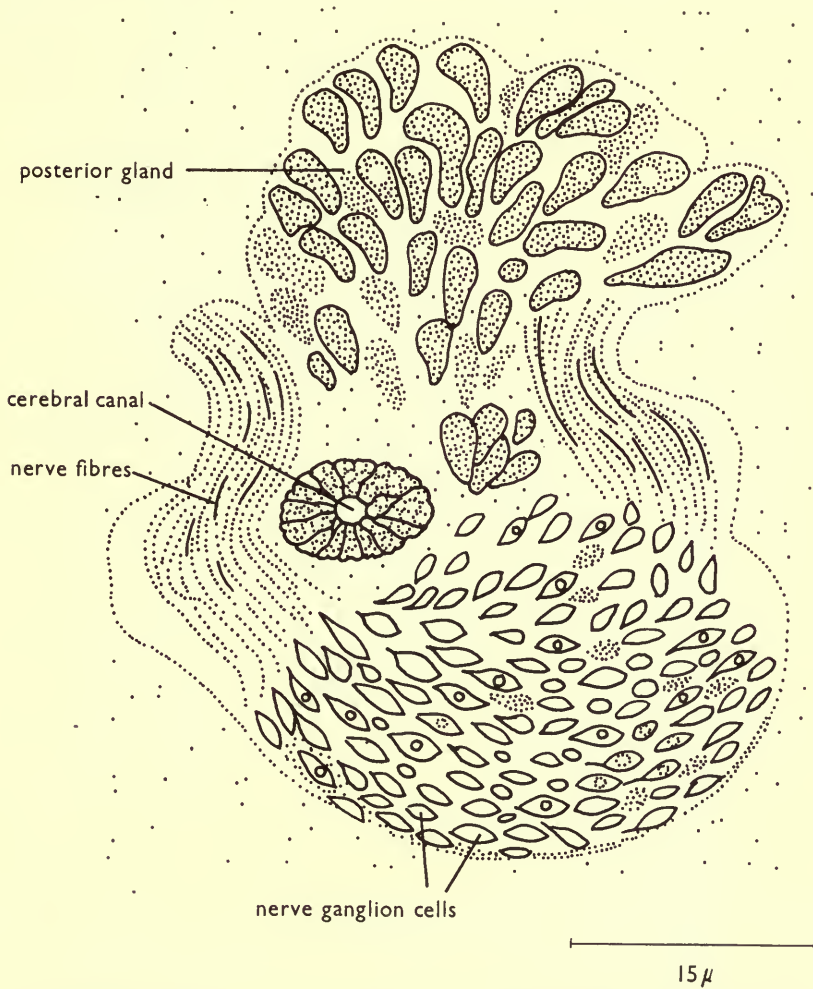


FIG. 5. Longitudinal section cerebral organ of *G. dendyi* to show the appearance of the posterior glandular region.

of extremely numerous nephridial pores over the surface of the animal (Pantin, 1947 : Hett, 1924). Examination of the late Professor Dendy's slides shows that the condition in *G. australiensis* is similar. It is different from that in the freshwater *Prostoma graecense* and from all marine nemertines, including *Prosorhochmus claparedii*.

9. The gut is of the general metanemertine type in which, however, the various

parts are subject to considerable variation. In *G. dendyi* and *G. australiensis* the oesophagus is short and merges into the stomach. The anterior gut-caecum is large and extends forward from the point of entry of the pyloric

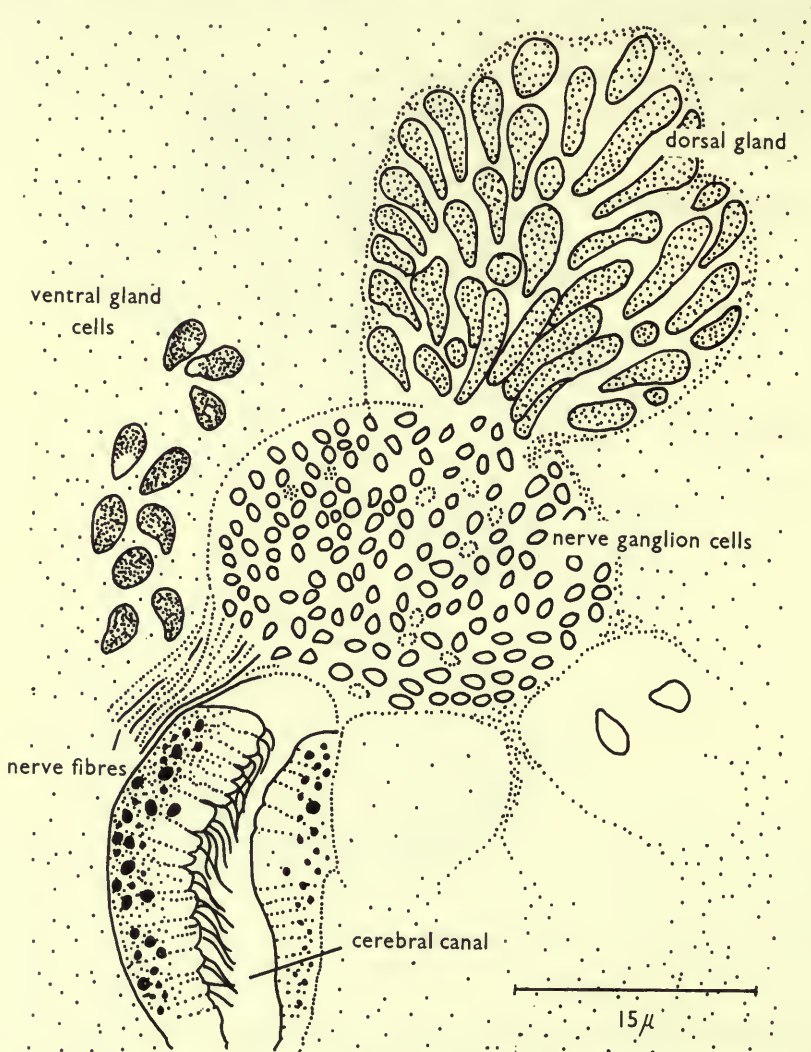


FIG. 6. Transverse section cerebral organ of *G. pelaensis* to show the appearance of the dorsal glandular region. Note beside the cerebral organ the ventral gland cells, cf. dorsal gland cells in *G. dendyi*.

tube into the stomach, and more or less divides into two short branches extending either side of it to the brain. According to Hett (1924), the condition in *G. hillii* is similar to *G. australiensis*. I can confirm the presence of the anterior caecum in *G. hillii*. The condition in these species may be

contrasted with that in the freshwater *Prostoma graecense* in which the caecum is short and gives rise to two long forwardly running branches. (Montgomery, 1895b, and personal observations.)

10. Large specimens are ♀, small ones are ♂ (Fig. 8). In *G. dendyi* this is apparently due to protandrous hermaphroditism. *G. dendyi* specimens of intermediate size (3–4 mm.) may have both degenerate testes and mature ova.

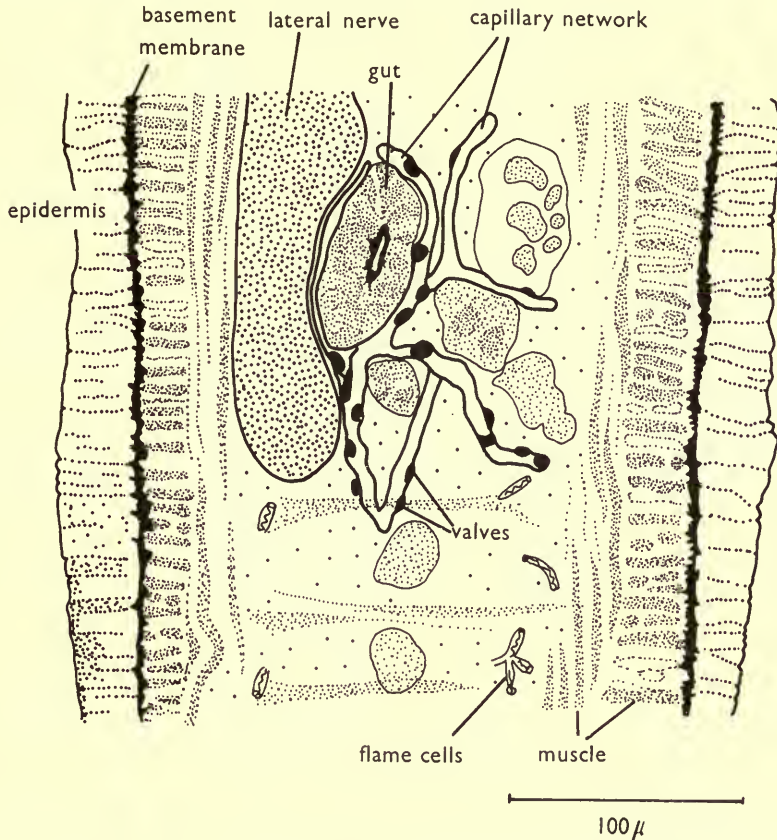


FIG. 7. Longitudinal section *G. dendyi* to show anastomosing subdermal capillary network.

11. All three species live in similar damp terrestrial situations which may be far from the sea.
 12. They all occur in southern Australia.

It is evident that these species share many characters which are rare among metanemertines and some which are unique. It is legitimate to infer that they are closely-related species.

The three species are not identical. *G. hillii* differs from the others in the colour pattern (purple brown with two bright red lateral bands in the anterior two-thirds of

the body), and in the very large number of eyes (80). In both the other species the ducts from the cerebral organ open into a transverse cephalic furrow on the ventral surface of the head in front of the brain. This furrow appears to be absent in *G. hillii* (see Hett, 1924). The nephridia are more numerous in this species than in

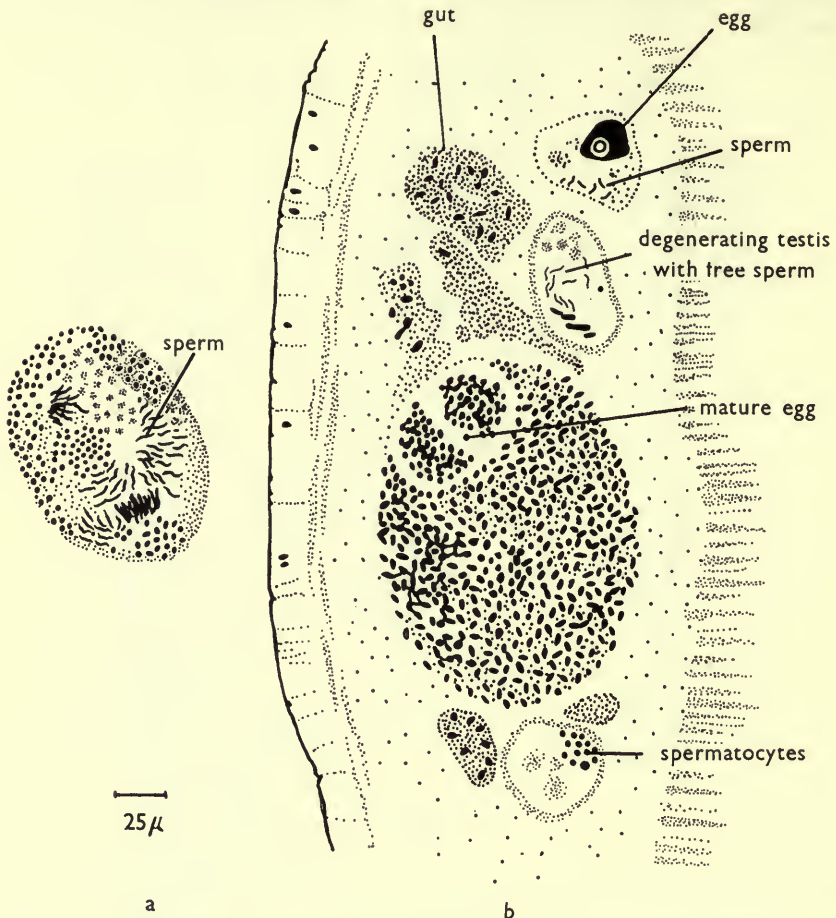


FIG. 8. Horizontal section *G. dendyi* to show sex organs : (a) mature testis ; (b) degenerating testis and mature ovary.

G. australiensis (see Hett, 1924). It differs from *G. dendyi* in the large number of stylet-sacs (5 against 2 to 3), the larger number of proboscis-nerves (18 against 11 to 15), and also in the very much more muscular body-wall. Two important distinctions I find between *G. hillii* and the other two species are the very much larger size of the accessory lateral nerve relative to the size of the lateral nerve itself, and the almost complete absence of the short lateral diverticula, which run forward from the anterior gut caecum to the brain in the other two species.

According to Hett, *G. hillii* possesses no cephalic gland. But re-examination of

the sections shows distinct though restricted masses of cells possessing the same histology as the cephalic glands in Dendy's original slides of *G. australiensis* (Fig. 9). The difference in development of the gland in the two species is great, and in the specimen of *G. hillii* examined the gland is confined to a dorsal portion behind the brain and two lateral or even ventro-lateral portions in front of it. This is very different from the great dorsal development over the brain in *G. australiensis* or even from the limited similar development I find in *G. dendyi*, but all three species in fact

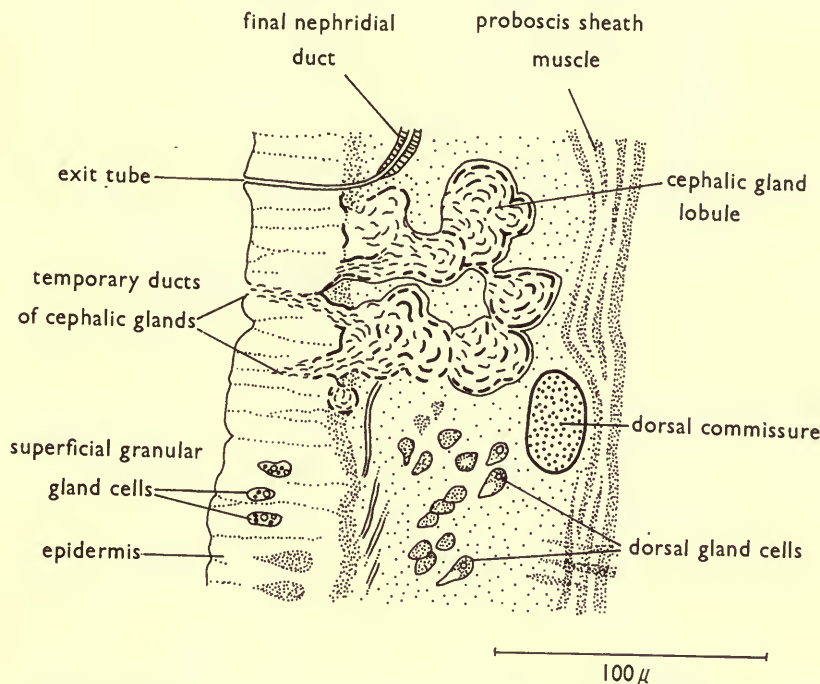


FIG. 9. Longitudinal section *G. dendyi* to show cephalic glands and dorsal gland cells (the bottom of the drawing is anterior).

possess this tissue, and it is similar also to that of the cephalic gland of *G. pelaensis* (see Schröder, 1918). This tissue in *G. australiensis* stains deeply with iron-haematoxylin. The tissue of corresponding structure in Miss Hett's slides does not appear to have done so. Whether this is due to a real difference in nature, or to a difference in the operation of staining, or to the decided variation of state of this gland, such as I have found in *G. dendyi*, remains to be seen, though the latter is the most likely explanation.

G. dendyi and *G. australiensis* are extremely similar. Many of their quantitative differences, e.g. number of eyes (30-40 in *G. australiensis* against 10-20 in *G. dendyi*), the number of stylet-sacs (2-5 against 2-3), the number of proboscis-nerves (16-19 against 11-15), may really be a reflection of the larger size of mature individuals in *G. australiensis* (up to 40 mm. against 10 to 25 mm.). But they also differ in colour pattern, a median dark brown band with or without slight lateral stripes in *G.*

australiensis against two brown lateral stripes only in *G. dendyi*: as Stephenson points out (1936), while colour may be very variable, pattern is of systematic importance. Further, *G. dendyi* possesses only a small cephalic gland. Dakin (1915) found none, and Stammer (1934) records it as "kaum entwickelt", but examination of my South Devon specimens shows a limited amount of lobular tissue of the typical large finely-granular secretory cells with small nuclei, which occupies the antero-lateral part of the head just as in the extensive cephalic gland-masses of *G. australiensis* (Fig. 10). The gland in *G. dendyi* is much smaller than the extensive

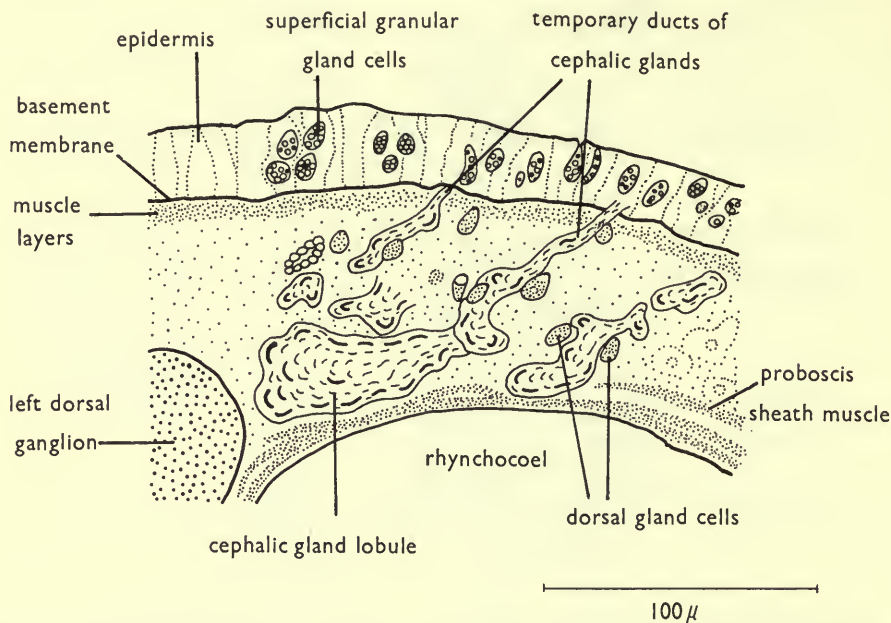


FIG. 10. Transverse section *G. dendyi* to show cephalic glands and dorsal gland cells (the bottom of the drawing is ventral).

structure figured by Dendy for *G. australiensis*, but not so much reduced as in *G. hillii*. It was noted that the size of the glandular tissue in *G. dendyi* varies in individuals, possibly in relation to the amount of recent secretion before fixation. Bürger (1897) has pointed out the relation of these glands to the production of slime round the head in nemertines.

There are other significant quantitative differences to be seen when sections of the two species are compared. In *G. australiensis* the musculature of the body-wall is much more developed than in *G. dendyi*; and though the latter possesses dorsal gland-cells similar to those found in the dorsal part of the head-region of *G. australiensis*, the cells are comparatively few and mostly scattered singly rather than in the well-defined groups figured by Dendy (1892) and clearly to be seen in his slides.

My examination of the three species shows that *G. dendyi* differs from both the other species in one other important respect. In both the others the posterior

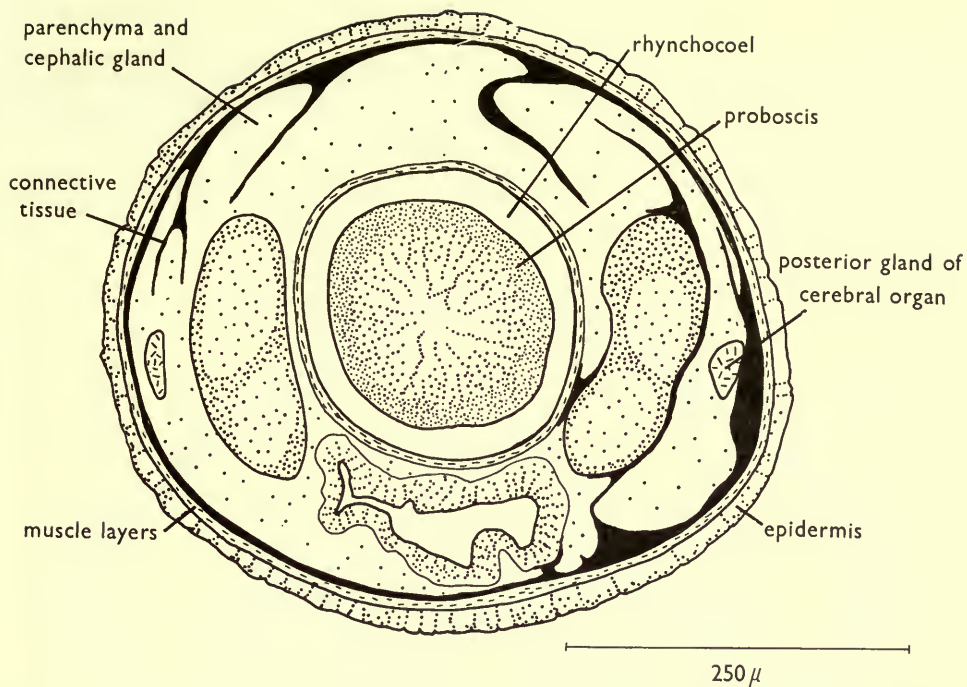


FIG. 11. Transverse section *G. dendyi* to show position of posterior glandular extension of cerebral organ.

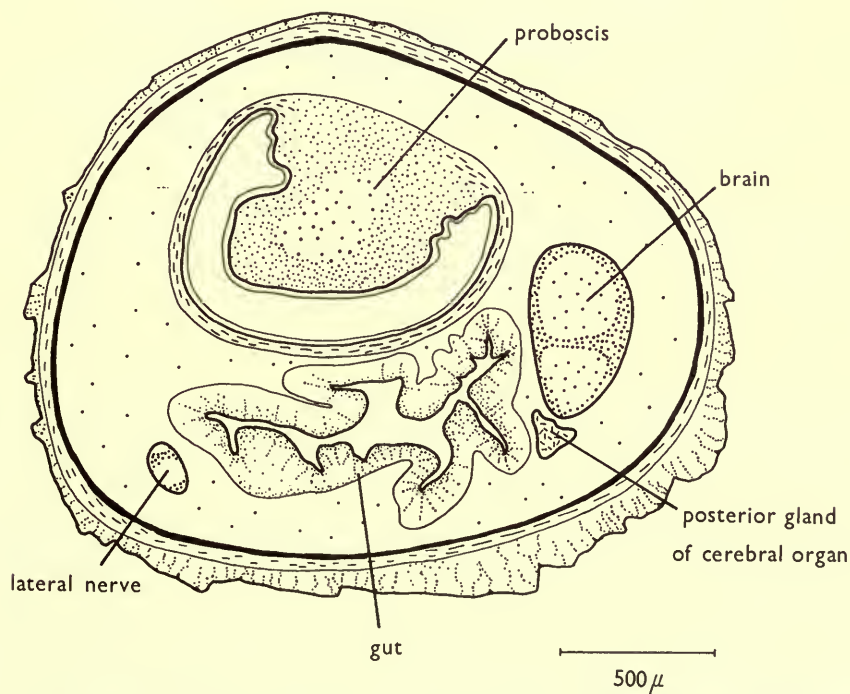


FIG. 12. Transverse section *G. hillii* to show position of posterior glandular extension of cerebral organ.

glandular extension of the two cerebral organs extends backwards below the beginning of the nerve-cords, so that they lie on each side of the oesophagus and merit Dendy's term "oesophageal organ". But in *G. dendyi* the extensions run more dorsal and are lateral to the base of the brain (Fig. 11).

From this we may conclude with reasonable certainty that *G. australiensis*, *dendyi* and *hillii* are distinct species of the same genus.

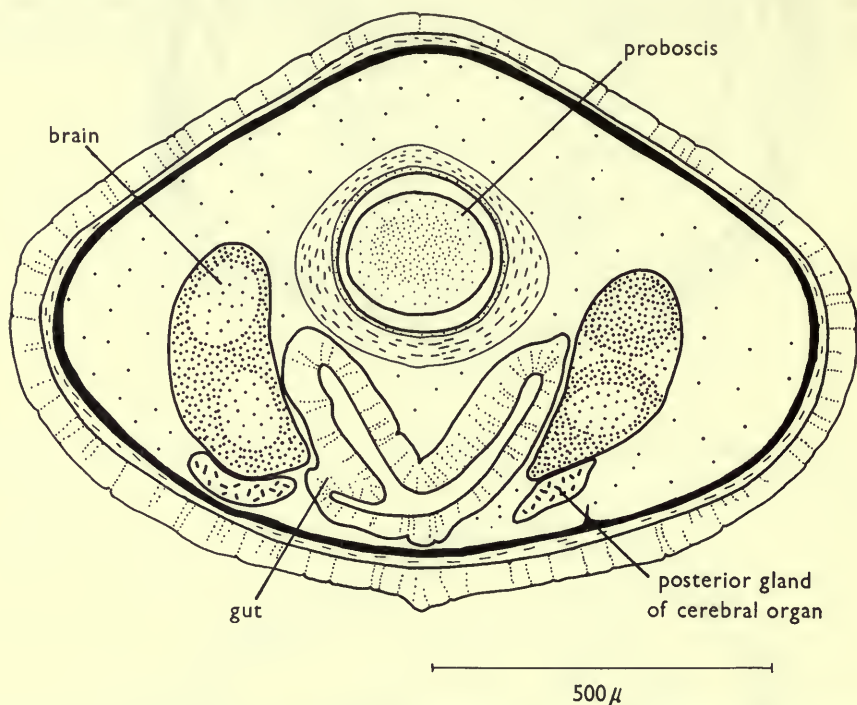


FIG. 13. Transverse section *G. australiensis* to show position of posterior glandular extension of cerebral organ.

THE PELAENSIS GROUP

Let us now compare the features of the Australian group of species with those of *G. pelaensis*. This animal has been fully described by Schröder (1918), Hett (1927) and Coe (1940), and I have also been able to examine the slides prepared by Miss Hett and by Dr. Wesley Coe and can confirm the major anatomical characters attributed to the species by these authors. Whilst there is a number of generalized metanemertine characters common to all, *G. pelaensis* and the Australian group share in addition certain special characters some illustrations of which will be found in Schröder's paper.

1. There is a slight tendency to multiplication of the eyes. The anterior pair remain single and large, but the posterior pair may be divided into two or three pairs of small eyes (Hett, 1927).

2. The ducts of the cerebral organ open ventrally into a transverse furrow.
3. A mass of gland-cells opens into the posterior, nervous, part of the cerebral organ. From Schröder's figure the cells evidently resemble those of the

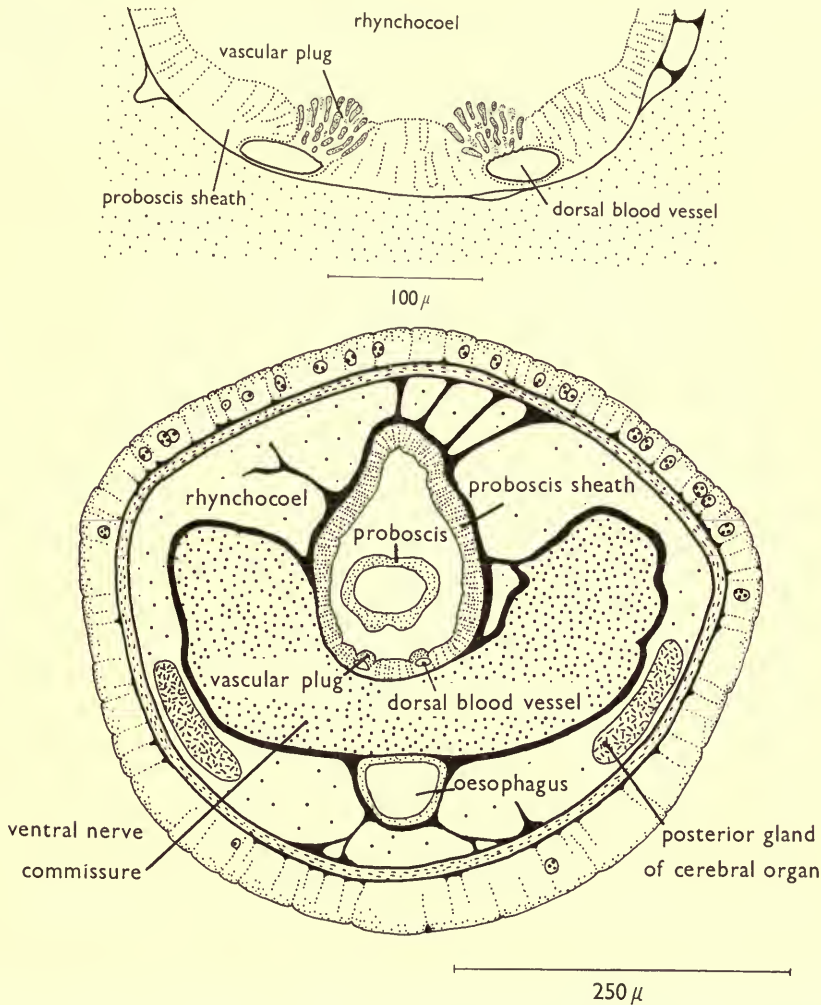


FIG. 14. Transverse section *G. dendyi* to show the two vascular plugs, from right and left branches of the dorsal blood vessel.

posterior glandular extension of the Australian species, though they are differently situated. I can confirm this (Figs. 4, 5, 6).

4. There is an accessory lateral nerve-tract derived from the dorsal ganglion, as in the Australian species, rarely found elsewhere in the phylum.
5. As in the Australian species, the dorsal blood-vessel in *G. pelaensis* enters the rhynchocoelic sheath. In this case the dorsal vessel itself carries a plug of tissue which separates it from the cavity of the rhynchocoel. In structure this

plug resembles the paired plugs of the Australian species, but there is only one such plug in *G. pelaensis* (cf. Fig. 17). A similar plug occurs in some other metanemertines, as in *Prostoma graecense* (see Böhmig, 1898) and in *Prosorhochmus claparedii* (Fig. 23).

6. In *G. pelaensis*, as well as in the Australian species, the protonephridia are extremely numerous throughout the body and, unlike many metanemertines,

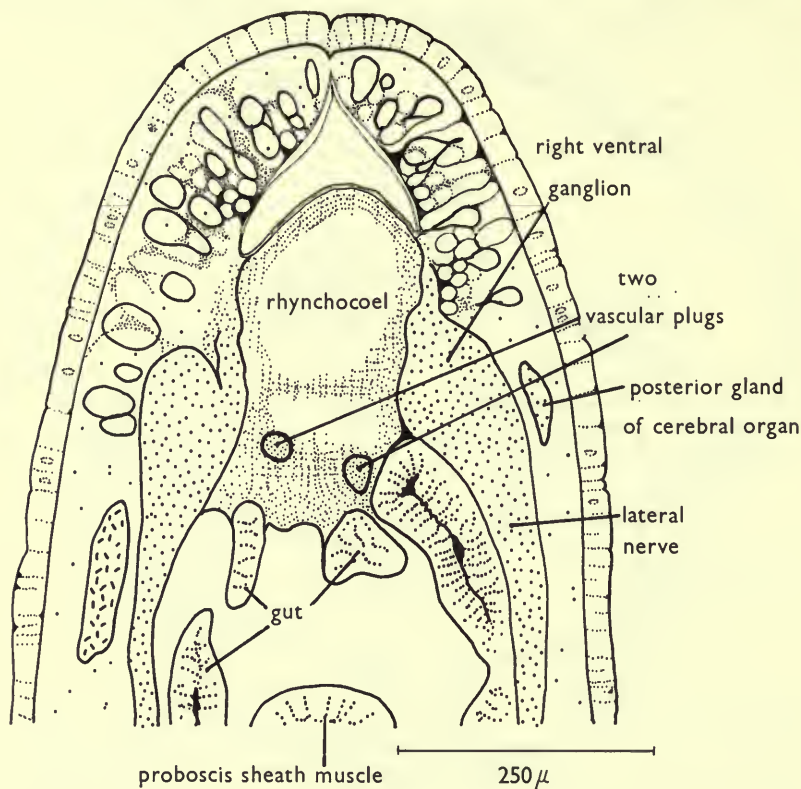


FIG. 15. Longitudinal section *G. dendyi* to show the two vascular plugs.

are not intimately in contact with the epithelium of the blood-vessels (Schröder, 1918; Coe, 1940), though they may be strongly aggregated in their neighbourhood. Near their exit the excretory canals show striation of the cytoplasm, recalling that of the whole of the last section of the excretory canal in the Australian species. The canals open to the exterior by many thousands of pores all over the surface.

7. *G. pelaensis* is a protandrous hermaphrodite. It undergoes subsequent repeated sex reversals (Coe, 1940); these have not been detected in the Australian species, but may exist.
8. *G. pelaensis* inhabits damp terrestrial situations which may be far from the sea.

These points together, particularly the common possession of an accessory lateral

nerve, lead to the conclusion that there is a significant relationship between *G. pelaensis* and the Australian group.

Geonemertes pelaensis, however, differs from the Australian species very much more than these differ from each other. Some of these differences are due to the retention of generalized metanemertine characters lost in the Australian species.

1. Though there is often some multiplication of the posterior pair of eyes, the eyes are much nearer the primitive tetrastemmatid condition of four eyes.

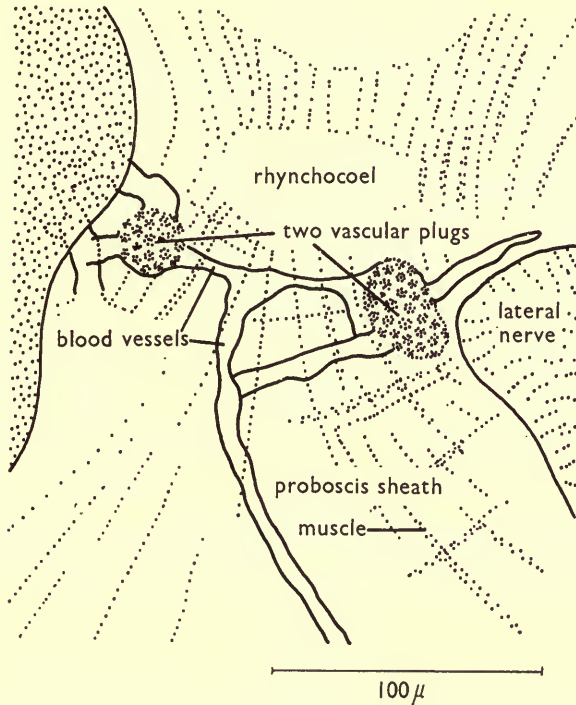


FIG. 16. Longitudinal section *G. dendyi* to show the two vascular plugs (further enlarged).

2. It is to be inferred from Schröder's careful description (p. 161) that *G. pelaensis* lacks "dorsal gland cells" corresponding to those of the Australian species. Schröder (1918) noted, however, the presence of large numbers of gland-cells ventrally and laterally placed in the head, particularly behind the transverse head-furrow. There is none dorsally. I have compared these cells with Dendy's "dorsal gland-cells" in *G. australiensis*, and though their situation and distribution is quite different, the histology of the cells is apparently the same (Fig. 6). The difference thus seems to be one of position and distribution, rather than presence or absence of a particular cell-type.
3. The frontal organ as well as the cephalic gland is retained and well developed.
4. The vascular system apparently includes commissures between the gut-pouches

(Schröder, 1918), as in many other metanemertines, and does not possess a subdermal plexus as in the Australian species.

G. pelaensis also differs from the Australian species in specialized characters.

1. The posterior glandular part of the cerebral organ does not extend backwards, as in the Australian species. It lies dorsal to the canal in the nervous part of the organ, which it envelops (see Schröder's (1918) figure 39 and see Fig. 4 here).
2. Though greatly developed in both in comparison with marine species, the nephridia of *G. pelaensis* differ very considerably from those of the Australian

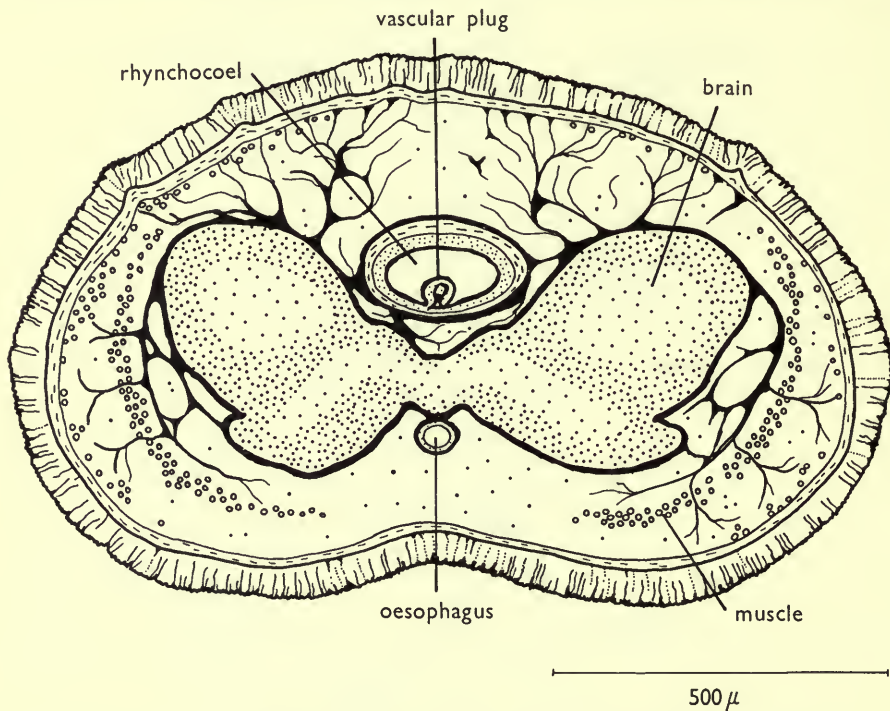


FIG. 17. Transverse section *G. arboricola* to show the single vascular plug.

species (Fig. 18). The protonephridia do not tend to occur in pairs, but each is itself a double structure. It has *two* nuclei at the head of the ciliary flame instead of one. The cilia of the flame often appear to arise from two roots, one beneath each nucleus. The cytoplasm of these nephridial cells appears rounded, rather than attached to the parenchyma by fine strands as in *G. dendyi*. The upper part of the capsule of the protonephridium is strongly supported by refractile, apparently cuticular, transverse, bar-like structures. Some traces of one or two transverse supporting thickenings of the wall may sometimes be seen under critical optical conditions in the protonephridia of *G. dendyi*, but their development cannot compare with that of the highly developed supporting structures of *G. pelaensis*. These structures consist of some seven strongly developed skeletal rings in the upper half of the protonephridium. The rings are divided

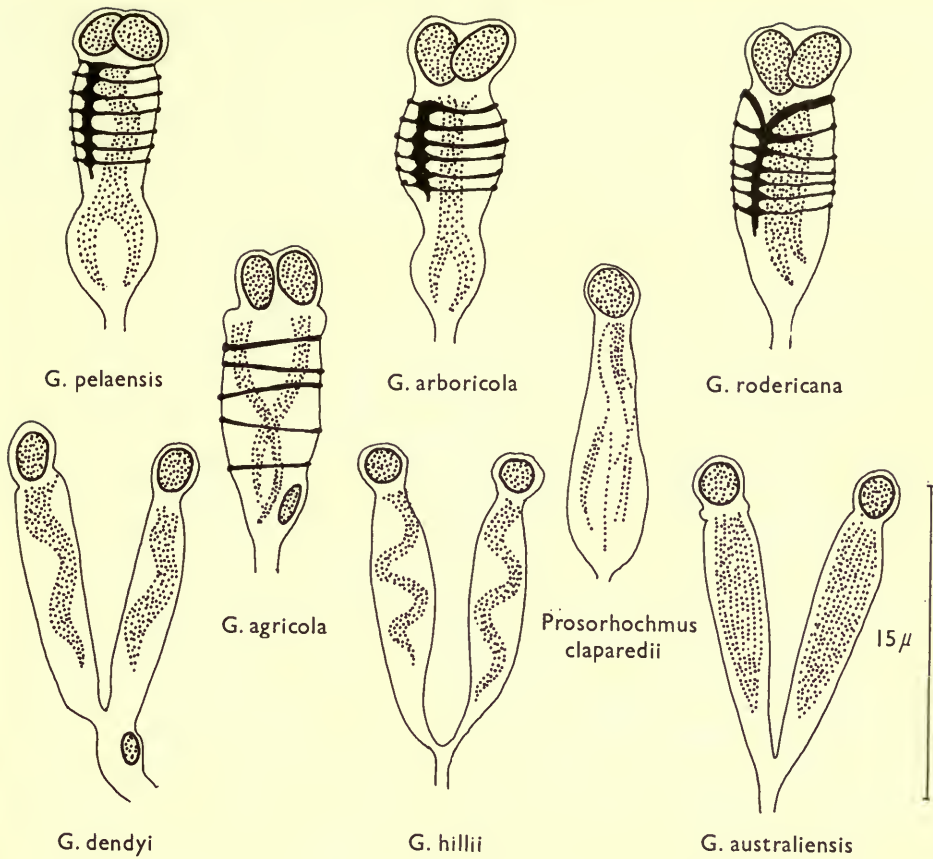


FIG. 18. Flame cells (see Fig. 18a for labelling).

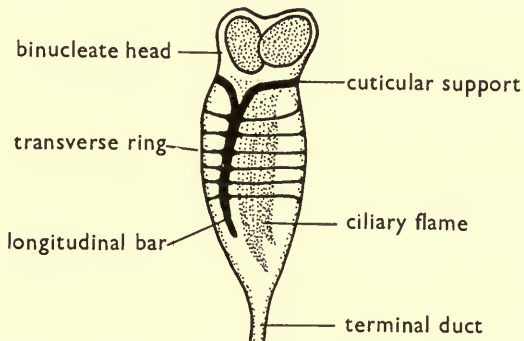


FIG. 18a. *G. rodericana* flame cell from Fig. 18.

into two halves by two vertical skeletal thickenings diametrically opposite each other in the line of the two nuclei, giving a "bivalve" appearance to the cuticular support (Fig. 18a).

Unlike the condition in the Australian species the protonephridia in *G. pelaensis* are not restricted to a superficial layer in the parenchymal spaces beneath the body-wall. They are found to some extent throughout the parenchyma, even between the rhynchocoel and the gut (Schröder, 1918). Certain parenchymal spaces, particularly along the course of the cephalic vascular loop which runs from the dorsal vessel into the tissue-spaces in the head, are packed with such vast numbers of protonephridia as to constitute "nephridial glands" (Coe, 1940) (Fig. 19). In

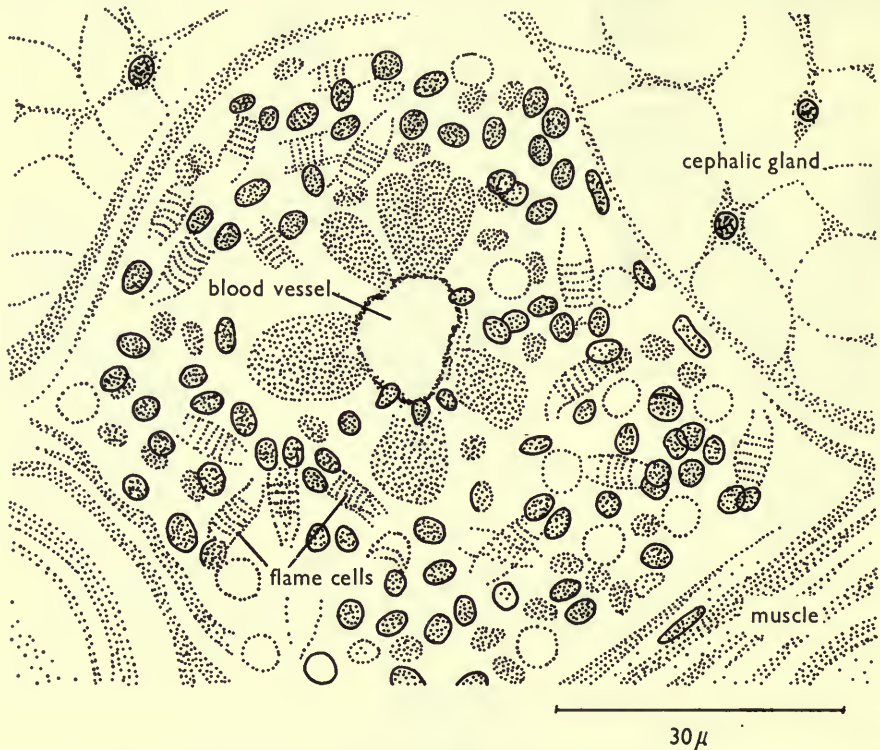


FIG. 19. Transverse section of head region of *G. rodericana* to show nephridial glands.

contrast, the protonephridia in *G. dendyi* are not directly aggregated round the blood-vessels, though the protonephridia, their ducts, and the superficial vascular plexus of this species are confined to a common layer immediately beneath the muscular body-wall.

Schröder points out (p. 10) that the end-canals of the protonephridia of *G. pelaensis* collect together in tubules following an irregular course. But there is no evidence of the well-defined convolution seen in end-canals of *G. dendyi*. The end-canals of *G. pelaensis* open into tubules with ill-defined walls of vacuolated protoplasm. The tubules lack the striking radial cytoplasmic striation of the second convoluted part of the nephridial canal in *G. dendyi*, and resembles rather the more generalized condition of the tubules in *Prostoma graecense* (Böhmig, 1898, Figs. 19-22) (Fig. 20).

The final relatively short exit canals of *G. pelaensis* do, however, show traces of coiling and also of radial striation (Schröder, 1918), which might perhaps be compared with the much more extensive second convoluted tubule of *G. dendyi*.

Whilst, therefore, there are points of resemblance between *G. pelaensis* and the Australian species, there are some striking differences, particularly in the organization of the nephridial system, which preclude the relation from being a very close one.

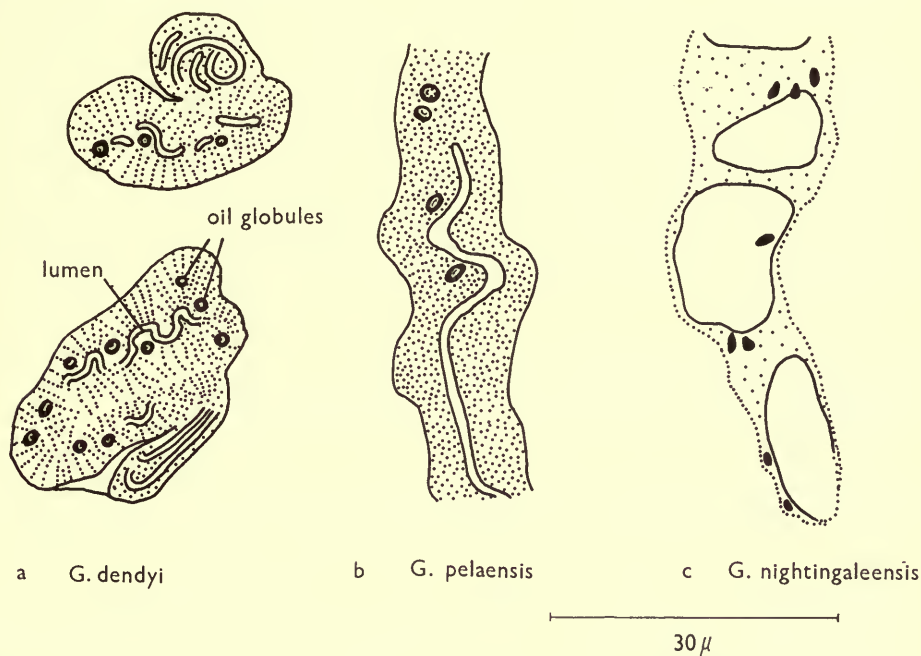


FIG. 20. Nephridial ducts of *G. dendyi*, *G. pelaensis* and *G. nightingaleensis*, showing the thick glandular walls with radial striation in *G. dendyi*.

We shall now pass to two species which prove to be extremely closely related to *G. pelaensis*, notwithstanding wide geographical separation. *Geonemertes arboricola* was partially described by Punnett (1907) from material collected from the Seychelles on the "Sealark" expedition. He noted some resemblance to *G. pelaensis*, and apart from a supposed absence of nephridia differentiated it only on colour-pattern and the reduction or absence of the posterior pair of eyes. Hett (1927) has pointed out that the examination of further specimens of *G. pelaensis* from Samoa shows that the colour pattern, based in both cases on a single brown dorsal stripe, and eye number of this species is variable and the condition described in *G. arboricola* is within the range of *G. pelaensis*. Punnett, however, found no evidence of an excretory system in *G. arboricola* and did not describe the blood-system.

Specimens and slides of *G. arboricola* in the Cambridge Museum collected on the Sealark expedition were examined. The slides were restained with Mallory's triple stain. Examination showed that *G. arboricola* possesses a well-developed nephridial system and that in this and in other features it resembles *G. pelaensis* very closely :

1. As Hett (1927) points out, the colour pattern and eye number of *G. arboricola* fall within the range of that of *G. pelaensis*.
 2. On examination of *G. arboricola* I find that like *G. pelaensis* it possesses a frontal organ and a well-developed cephalic gland.
 3. As in *G. pelaensis*, the "dorsal gland cells" of the Australian species are absent in *G. arboricola*, but again we find that there are cells ventro-laterally placed in front of the brain which are not unlike the "dorsal gland cells" in cytology.
 4. Both species possess a fairly well-developed cerebral organ, which with its gland is nearly as large as the dorsal ganglion. Punnett says the cerebral organ is small, but comparison of his figure (Plate 11, Fig. 3) with corresponding slides suggests that he was considering the cross-section of the canal of the organ only. Neither species has the large posterior "oesophageal" gland of Dendy, but both possess similar glandular material above the nervous posterior lobe of the cerebral organ. The ducts from the canal of the cerebral organ open ventrally into a transverse furrow in both cases.
 5. *G. pelaensis* is said to have two to four stylet-sacs, whilst Punnett records four in *G. arboricola*.
 6. An accessory lateral nerve is present in both.
 7. *G. pelaensis* is said to have 16 to 21 proboscis-nerves (Hett, 1927; Coe, 1940), whilst specimens of *G. arboricola* are described with nineteen.
 8. Examination shows that, like *G. pelaensis*, *G. arboricola* lacks a vascular subdermal network but possesses the more generalized lateral commissures running from the dorsal to the lateral blood-vessel between the gut-pouches.
 9. As in *G. pelaensis*, the dorsal blood-vessel enters the rhynchocoelic sheath and supplies one single plug of cells in the base of the rhynchocoel, just behind the level of the ventral brain-commissure. In *G. arboricola* (Fig. 17) the plug is longitudinally elongated ($40 \times 100 \mu$), and the vessel under the plug bulges into the rhynchocoel much more than do the flat circular plugs of the Australian species.
- Schröder's (1918) figure of the plug in *G. pelaensis* suggests that the dorsal vessel ends there. But though rather imperfect fixation of the material I have examined makes satisfactory observation a little difficult, it seems reasonably certain that the dorsal vessel in *G. arboricola* proceeds beyond the plug and branches before the point of entrance of the mouth into the rhynchodaeum. Each branch passes over the lower commissure of the brain and descends to run along the upper surface of the cerebral organ on each side. The branches then run forward towards the snout and, turning upwards, join to form the cephalic vascular loop. I have found a precisely similar system to this showing itself with great clarity in the slides of *G. rodericana* which I have examined (Fig. 22). Examination of Miss Hett's slides of *G. pelaensis* gives a fairly clear indication of the existence of the same arrangement and connexion of the cephalic vascular loop, notwithstanding Schröder's figure.
10. The nephridia of *G. arboricola* agree closely with Schröder's description for *G. pelaensis*. The protonephridia in their upper third have binucleate heads and seven strong transverse supporting half-rings, which connect with stout

vertical bars at opposite sides of the diameter along the line of the two nuclei, (Fig. 18) like those figured by Schröder. The protonephridia freely occupy the parenchymal spaces, and where these are restricted around the cephalic vascular loop by the greatly developed cephalic glands they form "nephridial glands" with vast numbers of protonephridia, as described by Coe (1940) in *G. pelaensis*. In both species the "glands" consist of a dense aggregation of protonephridia along the whole course of the cephalic vascular loop. Reference will be made to this when discussing *G. rodericana*.

In *G. arboricola* and *G. pelaensis* the nephridial end-canal systems are similar. There are numerous wide, highly vacuolated, separate collecting canals which apparently open separately by numerous canals to the exterior. In the Seychelles material the exit-canals can be traced to the basement-membrane, but the fixation of the ectoderm is not sufficiently good to justify with certainty the conclusion that the numerous narrow ducts, which are to be seen in the ectoderm, correspond to the openings of the nephridial exit-canals. The fixation of the specimens is unfortunately too poor to enable detection of any radial structure in the end canals.

11. Punnett (1907) states that *G. arboricola* is a simultaneous hermaphrodite. The specimens I have examined appeared to be female. The present evidence allows the possibility that it is a cyclical hermaphrodite like *G. pelaensis*, but does not prove it.
12. *G. arboricola* inhabits damp terrestrial situations which may be far from the sea.
13. The recorded sizes are not very different for such a variable character : 35–50 mm. for *G. pelaensis* against 15–25 mm. for *G. arboricola*.

The above observations leave no doubt at all that *G. pelaensis* and *G. arboricola* are very closely related. Indeed there is little anatomical evidence at present to suggest that they are specifically distinct. However, in view of the wide separation between their places of occurrence, in the New Guinea area and the Seychelles, and in view of the possibility that further work, particularly on the relations of the cerebral organ and on the vascular system, may serve to show specific differences, it would lead to confusion if they were now assigned to the same species.

Through the kindness of the authorities of the British Museum (Natural History), London, I have been able to examine material, including original sections, of Gulliver's species of *Geonemertes* (= *Tetrastemma*) *rodericana* (Gulliver). Gulliver (1879) gave a brief account of this species to which a few points were added by Punnett (1907). The former's account needs correction in that he said that the cerebral organs were absent, and the latter's in that he denied the existence of an excretory system. Both can in fact be demonstrated in the original sections.

G. rodericana is closely related by a number of features to *G. pelaensis* and *G. arboricola*. In *G. rodericana* :

1. There are two or four eyes (Punnett, 1907).
2. The cephalic gland and frontal organ are well developed.
3. True "dorsal gland cells" are absent ; though again there are cells of rather similar structure to them in the ventro-lateral region of the head.

4. The cerebral organ is similarly placed to that of the other species ; it is antero-ventral to the brain and opens by vertical ducts running to a transverse furrow on the ventral surface. There is again no glandular "oesophageal organ" of Dendy, though gland-cells of similar appearance lie above the nervous part of the cerebral organ.
5. Gulliver records four stylet-sacs.
6. There is an accessory lateral nerve. According to Punnett (1907) the lateral

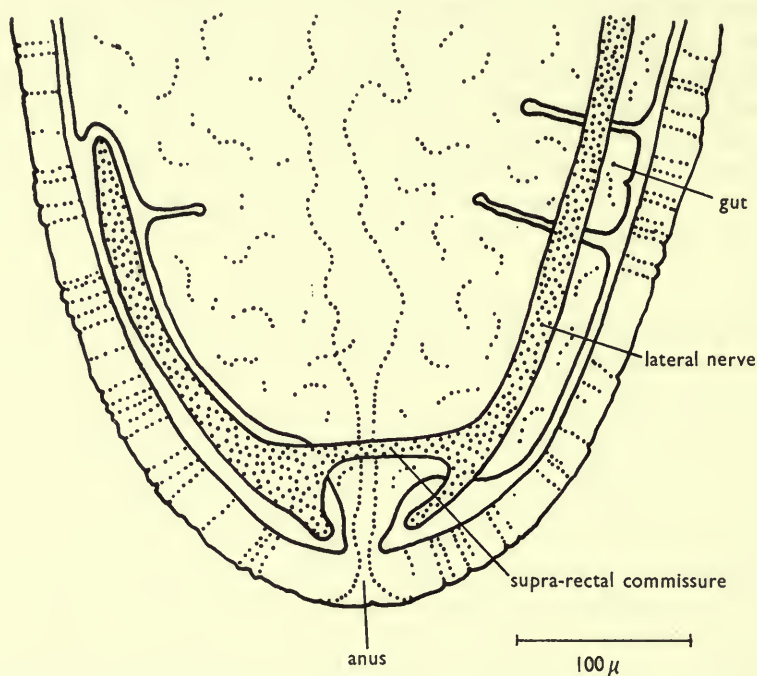


FIG. 21. Horizontal section anal end of *G. dendyi* to show supra-rectal nerve commissure.

nerves form a posterior supra-anal commissure in this species and in *G. arboricola*. I can confirm this, but this does not differentiate these species from the Australian species, because there is a small supra-anal commissure in *G. dendyi* (Fig. 21).

7. There are 19-21 proboscis-nerves (Punnett, 1907).
8. *G. rodericana* possesses the usual commissural vessels between the dorsal and lateral blood-vessels and does not possess the vascular subdermal network of the Australian group.
9. The dorsal blood-vessel enters the rhynchocoel sheath and supplies a single tissue plug in the base of the rhynchocoel just behind the level of the ventral brain-commissure (Fig. 17). It is elongated as in *G. arboricola*, and, as in the latter, the dorsal vessel branches forwards beyond to give the cephalic vascular loop (Fig. 22).

10. The nephridia resemble those of *G. pelaensis*. The protonephridia have binucleate heads and strong transverse supporting rings divided by two longitudinal bars (Fig. 18). The distribution of the protonephridia in the body is similar to that in *G. pelaensis*. The canal system resembles that of *G. pelaensis*.

The relation of the nephridia to the cephalic vascular loop is particularly striking in *G. rodericana*. The loop runs down on each side from the anterior end of the dorsal vessel to the cerebral organ. Each arm then runs forward almost to the anterior end of the head; bends backwards and upwards

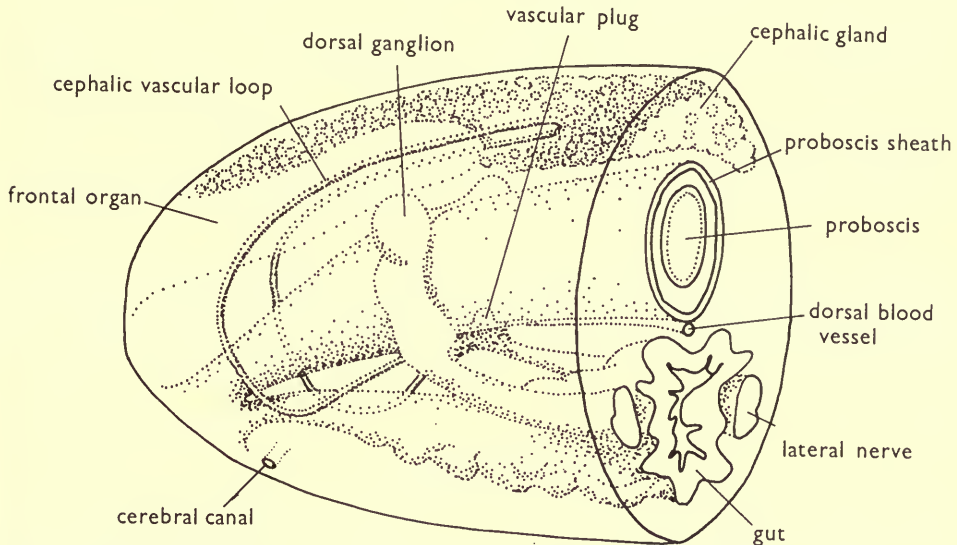


FIG. 22. Reconstruction of anterior end of *G. rodericana* to show cephalic vascular loop (cerebral organs not shown).

through the dorsal part of the head, till they join to complete the loop at a level just behind the brain. Throughout their course the arms of the loop are surrounded by a dense highly localized layer of protonephridia, giving the vessel a very striking appearance (Fig. 19). We have noted that a similar vessel is seen in *G. arboricola* and *G. pelaensis*.

Schröder remarks on the close relationship of blood-vessels and protonephridia in the head of *G. pelaensis*, but he seems to consider it as no more than the accidental restriction of both blood vessels and protonephridia to exiguous tissue spaces in the parenchyma. The relation of these structures in *G. rodericana* is far too clear to be accidental: the protonephridia form a dense localized layer round the vessel, which precisely marks its course; and it is worthy of note that Coe's (1940) figure and description of the condition in *G. pelaensis* suggest a more definite relation than Schröder's account suggests.

It is interesting to note in passing the almost invariable close relationship of the geonemertine vascular system with any structure where much water may be secreted. This is true of the rhynchocoelic cavity, the cerebral

organs, the nephridia and also the cephalic gland, alongside of which runs the cephalic vascular loop. The relation suggests that water may be transported to these organs from the body of the parenchyma (cf. Pantin, 1947).

11. Punnett (1907) records that *G. rodericana* occurs as male and female.
12. *G. rodericana* inhabits damp woods. It is killed by immersion in sea water (Gulliver, 1879).
13. Punnett (1907) gives its size as 27–75 mm.

The closely similar character of *G. rodericana* to *G. pelaensis* is as clear as its difference from the Australian group.

G. rodericana has certain minor points which differentiate it from *G. pelaensis* and *G. arboricola* :

1. The colour is dark green with a single median white line and four white spots (round the eyes) on the head.
2. In the specimens examined the cerebral organs are rather smaller than those of the other two species.

As with *G. arboricola*, the differences of *G. rodericana* from *G. pelaensis* are small and further work is needed to establish the validity of their distinct specific rank, apart from their known minor differences and their widely separate habitat. In any case, the essential similarity of plan in species from widely separate oceanic islands is most remarkable.

G. chalicophora

This species is only known from European greenhouses (Stammer, 1934). Of all the terrestrial nemertines that have been described, *G. chalicophora* has the least number of specialized characters. Böhmig's (1898) description of it is full.

1. It possesses four eyes, the simple metanemertine condition.
2. The cephalic gland is well developed, though as in *G. australiensis* the frontal organ is missing and the gland opens by extempore channels in the dermis of the head. Böhmig makes no reference to structures equivalent to dorsal gland-cells.
3. The cerebral organ is well developed, and is similar to that of the freshwater *Prostoma graecense* with which it is compared by Böhmig. Böhmig remarks that in comparison with those of *G. australiensis*, the posterior glands of the cerebral organ are strikingly absent in *G. chalicophora*, though he notes the presence of some such gland-cells in *Prostoma graecense*. The ducts of the organs are rather long (180 μ) and open ventrally, as in all the species so far mentioned, and open directly to the exterior. A transverse head-furrow is not described.
4. Like the other *Geonemertes* species we have described, there is an accessory lateral nerve.
5. The vascular system retains the quasi-metameric commissures linking the lateral and dorsal vessels and has no subdermal network (v. Graff, 1879).

6. The dorsal vessel enters the muscle of the rhynchocoel, but does not connect with a plug protruding into that cavity. Böhmig contrasts this with the condition of *P. graecense* which, as he shows, possesses a single plug.

This absence of direct contact between dorsal vessel and rhynchocoel is not very common in metanemertines, but occurs in a few genera, such as *Oerstedia*. Doubtless the absence is a secondary loss.

7. The protonephridia are simple structures with one nucleus at the head and no complex skeletal supports. They connect by a system of end-canals with paired lateral longitudinal canals which open to the exterior by some ten orifices on each side, a number far smaller than in any other species of *Geonemertes*. The whole condition is, according to Böhmig, closely comparable to that in *Prostoma graecense* : and, particularly in the unbroken longitudinal canals and in their simple histology, they are much less specialized than anything we have so far seen in *Geonemertes* species. [The flame-cells of *P. graecense* show a tendency which may throw light on the origin of binucleate flame cells like those of *G. pelaensis* ; for Böhmig figures pairs of fused flame-cells with two nuclei at the head, from which arises a double-rooted ciliary flame.]
8. Of the sexes little is known. Böhmig only records the presence of females.
9. Notwithstanding its lack of special modifications, the animal is well adapted to damp terrestrial conditions, having been found in various European green-houses though never in the wild state.

The chief characters of *G. chalicophora* which tend to relate it to the Australian and *Pelaensis* groups are the possession of an accessory lateral nerve (Böhmig, 1898) (Brinkmann points out the common error of its supposed absence in this species) ; and the ventral-running ducts of the cerebral organs. It lacks the other specialized features shared by the two groups. In many points it resembles the New Zealand species and *G. nightingaleensis* : the loss of the vascular plug might be secondary (cf. *Oerstedia* (Stiasny-Wijnhoff, 1930)).

G. agricola

G. agricola has been fully described by Coe (1904). It is to be found in Bermuda only, and I was able to obtain a few preserved specimens collected by Dr. Brian Boden in the summer of 1951. This species has a number of peculiarities, and except on one point my worms agree completely with Coe's excellent description.

In the first place this species has a number of unspecialized features. Among these we may note :

1. The possession of four eyes.
2. The presence of a well-developed frontal organ, as well as a cephalic gland.
3. The presence of quasi-metameric commissures between lateral and dorsal blood vessels.

But we are also confronted with a number of striking differences from all the species which we have considered :

1. The cerebral organs are anterior rather than ventral to the brain, and their ducts open antero-laterally instead of ventrally.
2. These ducts open just below a pair of lateral head-furrows which begin from the anterior end at the place where the frontal organ opens into the mouth and rhynchodaeum. As Coe points out, the ducts do not enter these head-furrows. But staining with Mallory's triple stain shows that each opens on to a very shallow channel of specialized ciliated epithelium which stains deep red. This channel continues forward parallel but below the head-furrow and ends before reaching the snout. This is quite a different arrangement from the single ventral transverse furrow of all the other species. But the condition in *G. agricola* is essentially the same as that which I find in *Prosorhochmus claparedii*.
3. There is no accessory lateral nerve. Brinkmann points out that Coe's (1904) original account leaves the matter in some doubt, but its absence is clearly shown by Coe both in his Fig. 18 (Plate 25) of a late embryo in his 1904 paper and in his Fig. 4A of an adult in his 1939 paper.
4. Coe describes the dorsal blood-vessel as failing to enter the walls of the proboscis-sheath at any point in its course. I find, however, that at one point just behind the brain it runs for a short distance immediately below the rhynchocoel, and from its upper surface there is a mass of cells histologically comparable to those of the vascular plugs of all other species of *Geonemertes* and also *Prostoma graecense* and *Prosorhochmus claparedii* (Figs. 23 and 24).
5. Though a cyclical hermaphrodite (Coe, 1904, 1939), as in *G. pelaensis*, the worm differs from all other species of *Geonemertes* in being viviparous. Again in this it resembles *Prosorhochmus claparedii*.
6. The animal, though terrestrial, is confined to the littoral region of the oceanic island of Bermuda (which possesses little natural fresh water). Unlike *G. dendyi* it is killed by prolonged immersion in fresh water but survives prolonged immersion in sea water (Coe, 1904), and occurs between tide-marks (Crozier, 1917). We may note that *Prosorhochmus claparedii* at Plymouth extends to crevices at the top of the Pelvetia zone, where it accompanies collembolids, myriapods, chernetids and gastropods transitional to land forms.

There seems little doubt in the face of this that *G. agricola* is widely separated from all other species mentioned and only possesses in common with them all the general metanemertine characters. It might well have evolved the terrestrial habit independently, as Coe (1904) suggests, and this is particularly probable because of its close resemblance to the genus *Prosorhochmus* in precisely those features in which it differs from other *Geonemertes*.

Whilst *G. agricola* possesses features which serve to remove it from all other species of the genus, it possesses one which remarkably enough it has in common only with the *pelaensis* group. Scattered through the parenchyma are binucleate protonephridia with heavy ring-like cuticular thickenings (Coe, 1929). These thickenings are six to eight in number and are arranged as circular, or possibly spiral, bars at regular intervals across the upper half of the protonephridial chamber. Coe (1929) remarks that these bars extend considerably further down the chamber than in *G. pelaensis*,

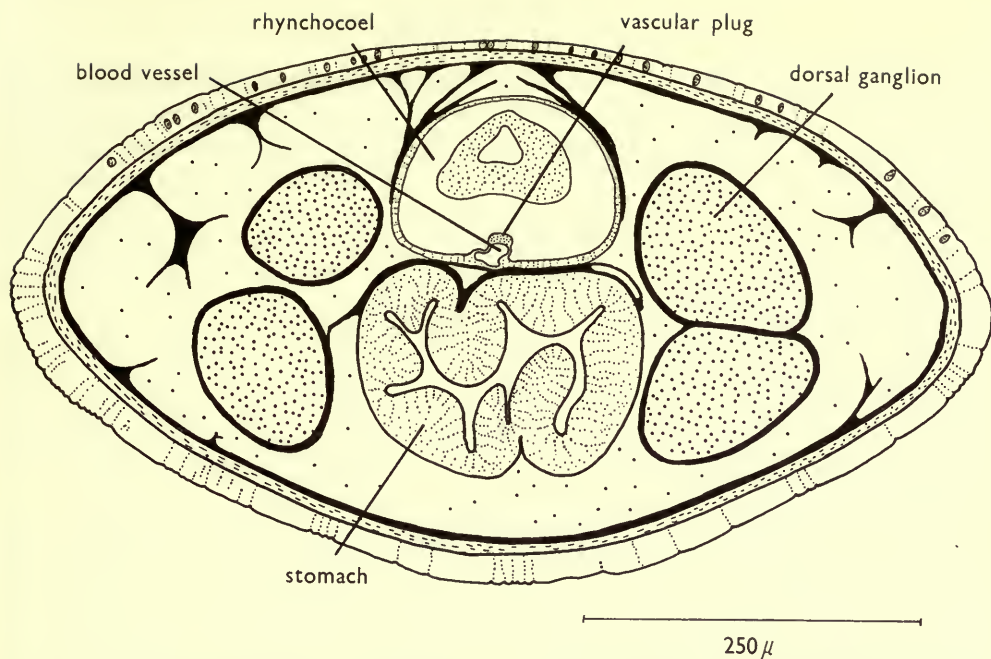


FIG. 23. Transverse section *Proisorhochmus clapedii* to show the single vascular plug.

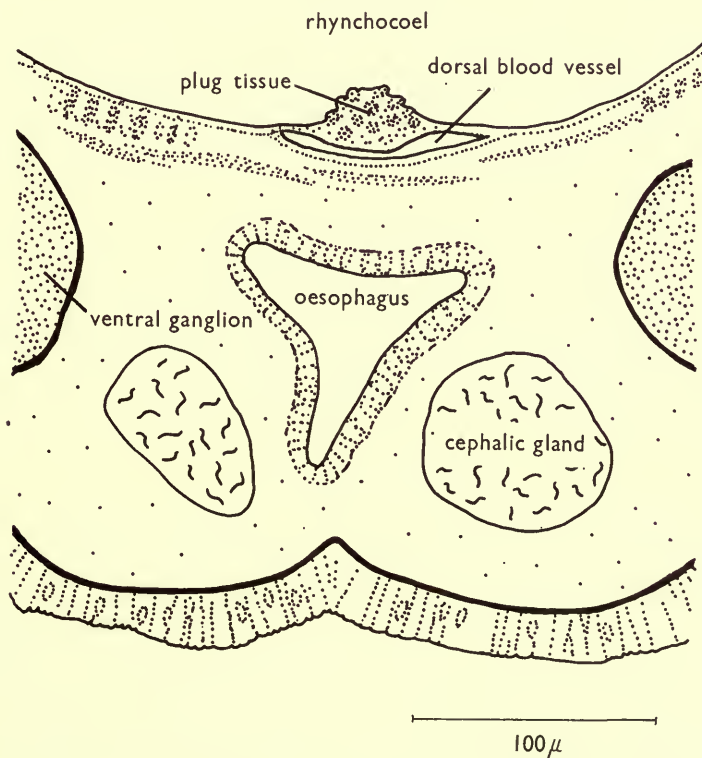


FIG. 24. Transverse section *G. agricola* to show tissue similar to vascular plug.

and a comparison of his figure with that of Schröder (1918) shows that the bars are much closer together near the head of the protonephridium in *G. pelaensis* (and *G. arboricola*) (Fig. 18). Like *G. pelaensis*, the protonephridia of *G. agricola* may have a longitudinal bar. But there is only one in this case and it is not very prominent. Coe's figures and account do not give the impression of an almost "bivalve" striated structure such as is present in *G. pelaensis* and *G. arboricola*. But in general the resemblance is striking. I can confirm all these observations by direct comparison between *G. agricola* and species of the *pelaensis* group.

The scattered protonephridia occur throughout the parenchymal spaces, including all sides of the proboscis-sheath and the gut. They are most numerous above and below the nerve-cord. Apart from the fact that Coe does not record any great aggregation into "nephridial glands" in the head, the condition seems very like that of *G. pelaensis* and does not show the special restricted sub-dermal distribution of the Australian species.

Coe's (1904 and 1929) accounts of the nephridial system show that this consists of end-canals which unite and join a number of separate convoluted main canals with thick walls. These main canals open to the exterior by some hundreds of openings. These features of the canal system resemble those of *G. pelaensis*, though the resemblance is perhaps rather due to a relative lack of specialization, as compared with the nephridia of the Australian group, than to a unique similarity such as we see in the barred protonephridia. For the canal system resembles in many ways that of *G. chalicophora*, and as Coe (1930) points out is derivable from a general metanemertine condition. The structure of the canal system is not so very different from that of a metanemertine like the freshwater *Prostoma graecense*, except for the break-up of the main canal into separate units and some increase in the number of exit canals (some hundreds), though this is far less than in *pelaensis* or the Australian groups (tens of thousands).

The nephridial canal system in *agricola* resembles also that in *Prosorhochmus clapedii*, except that in the latter the nephridia are confined to the head-region and apparently open by only a few openings on each side. Further, the protonephridia of the *clapedii* are simple and uninucleate (Fig. 18). If *agricola* is truly related to it then, for all their complexity, the occurrence of barred binucleate protonephridia in both *agricola* and *pelaensis* must be accounted convergence.

G. nightingaleensis

There is one other species which has received adequate description, *G. nightingaleensis* Brinkmann. The only important feature which Brinkmann left unstudied was the nephridial system. Through the good offices of Dr. Brinkmann, Mr. Nils Knaben of the Universitets Zoologiske Museum, Oslo, very kindly sent me a specimen of this interesting species collected from Nightingale Island, Tristan da Cunha, by the Norwegian Scientific Expedition, 1937-38. This specimen was sectioned: the anterior end vertically and the remainder transversely and horizontally. In sections stained with Mallory's triple stain, Azan or Masson's Haematoxylin Ponceau-light green method, the major features of the excretory system are clearly brought to

light, as is also the circulatory system. The following notes on the anatomy of the species are based on Brinkmann's account and upon these sections.

G. nightingaleensis possesses many unspecialized metanemertine characters and its various characters are shared with other species in a manner not easy to interpret.

1. It possesses the four tetrastemmatid eyes.
2. As in *G. chalicophora* and the Australian group, the frontal organ is lacking and the cephalic gland, which is well developed, opens by many apparently temporary ducts in the dorsal region of the head.
3. The cerebral organ is very small, as it is in *G. agricola* (see Coe, 1904), but it is differently situated, being ventral as in the other *Geonemertes* species. But compared with all other species, the organ is very reduced. It is thin ($90\mu \times 20\mu$), and flattened against the ventral surface of the brain (Fig. 3). The duct is so short that it leads at once into the organ, and there is no obvious cavity corresponding to the anterior sac of the gland, as described by Böhmig in *G. chalicophora* and present in others such as *G. dendyi* (Fig. 3).
4. The ducts of the cerebral organ open ventrally as in all species except *G. agricola*, and into a transverse furrow which is incomplete in the middle line.
5. There is no accessory lateral nerve. In this the species resembles *G. agricola* alone.
6. The lateral vessel connects with the dorsal by the usual quasi-metameric commissures, which are only found modified in the Australian group.
7. The dorsal vessel can be traced to two tissue-plugs in the base of the rhyncho-coel near the ventral commissure of the brain. In this the worm specially resembles the Australian species with their two plugs (Fig. 14).
8. The protonephridia occur typically in pairs and retain the simple condition with one nucleus in the head and no supporting ribs; as typically in *G. chalicophora* and the Australian group, but unlike *G. agricola* and the *Pelaensis* group (Fig. 18).
9. Unlike the condition in the Australian group, the protonephridia of *G. nightingaleensis* are scattered through the spaces of the parenchyma. There is, however, a definite tendency for aggregation of protonephridia into a stratum below the muscle-layer. While this slightly recalls the condition in the Australian species there is another feature of the distribution of the protonephridia which calls to mind the condition in the *Pelaensis* group. The protonephridia tend to be somewhat aggregated round the blood-vessels. There is, however, little or no aggregation round the cephalic vascular loop; a structure which is rather poorly developed and hard to follow in the specimen I have examined. On the other hand there is a dense aggregation of protonephridia between the base of the brain and the ventral surface, behind the cerebral organ. This is developed about a blood-vessel, which appears to be the anterior end of the lateral vessel, along the whole course of which there is some aggregation of protonephridia. The resemblance to *G. pelaensis* is thus rather in a general tendency of nephridial aggregation round blood-vessels and not in any specific aggregation round the cephalic vascular loop. A similar

aggregation is seen near the lateral vessels just behind the brain in the *Proso-rhochmus* I have examined.

The end-canal and duct system of the nephridia is less specialized than that in the *Pelaensis* group, and much less so than that of the Australian species. It recalls rather the condition in *G. chalicophora* and in *G. agricola*, the end-canals joining to form irregular coils which open into one of a number of fairly thick-walled coiled main canals which pass to the body-wall and empty by numerous pores to the exterior (Fig. 20). Altogether the whole excretory system resembles the relatively unspecialized condition in *G. chalicophora* rather than any other species.

10. The animals have either separate sexes or are perhaps protandrous hermaphrodites.
11. As in *G. agricola*, the species inhabits a region just above the tide level, and resembles it also in being found on an isolated island in the Atlantic Ocean (Nightingale Island, Tristan da Cunha).

This species brings out clearly the most puzzling features in the genus. Apart from the evident close relation of the species respectively within the Australian and *Pelaensis* groups, it is scarcely possible to find any major characters which divide the group in a way consistent with a division based on any other major character.

G. novaezealandiae

[See Appendix, where the author's draft has been expanded to include subsequent information. Ed.]

G. graffi, *G. spirospemia* and *G. caeca*

It is not intended to discuss in detail the remaining species since their descriptions are quite inadequate. *G. graffi* (Bürger, 1896) and *G. spirospemia* (Darbishire, 1909) possess four simple eyes and are believed to have an accessory lateral nerve. These are points in common with the *pelaensis* group and *G. chalicophora*. But without knowledge of the vascular and excretory systems no more can be said; and Darbishire's description of the accessory lateral nerve as "a ganglionic strand running along the dorsal surface of the nerve-cord" raises the suspicion that he was really referring merely to the normal dorsal layer of ganglion-cells of the lateral nerve itself. The question must be left in this vexing position till we have more material. Nothing is known of *G. caeca* (Darbishire, 1909) which would enable a new organism certainly to be identified as belonging to this species.

DISCUSSION

We now possess sufficient knowledge of ten of the species of the genus to permit us to consider their relationship. It is clear that *G. pelaensis*, *G. arboricola* and *G. rodericana* on the one hand and *G. dendyi*, *G. australiensis* and *G. hillii* on the other form each of two very closely related groups of species. The two groups show a

limited resemblance to each other. What is known of *G. novaezealandiae* (see Appendix) strongly suggests close relation with the Australian group. The relation of the *pelaensis* and Australian groups to the remaining species is, however, very curious.

The following table shows the distribution of the characters common to more than one species or group of species. The retention of a morphological character in the generalized metanemertine condition is represented by O. The suppression of such a character is represented by — and the appearance of a new or modified character by +. Special characters restricted to one species or group alone are not shown.

There are several clear morphological characters which could be used to divide the group, but the resulting divisions are mutually inconsistent. All the Indo-pacific species have an accessory lateral nerve. The presence of such a tract is of great morphological significance. When the complex relations of a nervous structure to sensory and motor organization are considered it is evident that the chance of the independent evolution of such a structure is much less than that of what may be a genetically simple character, such as colour-pattern or the mere suppression of a structure like the frontal organ. It should, however, be remembered that the degree of development of the tract varies greatly. It becomes steadily reduced as we pass back along the body of the animal. And at any level it is more highly developed in some species than in others; compare its weak development in *G. dendyi* with the strong development in *G. hillii* (Fig. 2, just before the anterior end of the gut caecum). [See Appendix for re-assessment of this character].

Whilst the presence of an accessory lateral nerve separates the Indo-pacific from the Atlantic species, other characters cut across this division. A number of characters distinctive of the Australian group are to be found in *G. nightingaleensis*; notably the simple nephridia, the absence of the frontal organ and in particular, the double rhynchocoelic vascular plugs. The *pelaensis* group does not share these characters. Still more remarkable the *pelaensis* group of the Indo-pacific appears to share two characters with *G. agricola* from Bermuda alone. The retention of the frontal organ is not very remarkable as a common feature; but the presence in both of binucleate flame-cells with skeletal supporting bars is very strange, and especially so because in every other respect *G. agricola* stands far apart from all the other species.

Nor do our difficulties end here, for when to the others we try to relate *G. chalicophora*, that species of unknown origin and of many generalized characters, we find further inconsistencies. *G. chalicophora* differs from *G. nightingaleensis* in that the dorsal vessel does not form any vascular plugs in the rhynchocoel, let alone a pair after the Australian pattern. It is thus presumably more generalized than *G. nightingaleensis*. But on the other hand it already possesses the accessory lateral nerve which is not to be found in that species.

If we attempt to make a "natural" classification on traditional evolutionary lines we find that whichever way we make it we have to assume that more than one character has been independently evolved. We might for example suggest that *G. agricola* is distinguished from the other species by so many features that it is probable that its binucleate barred flame-cells are evolved independently from those of the *pelaensis* group. One might point to the parallel of the nematocysts of

TABLE I
SUMMARY OF GEONEMERTINE CHARACTERS (including material from Appendix)

O = retention of primitive Metanemertine state. + = special Geonemertine character. — = suppression of character.

	Indopacific (I), Atlantic (A) or Southern (S)	Terrestrial (T), Littoral (L) or Freshwater (FW)	Viviparous (V) or Oviparous (O)	Multiplication of eyes (+)	Canal of cerebral organ Ventral (+) or Lateral (O)	Cephalic furrow transverse (+)	Rhynchocoelic vascular plugs (O, 1 or 2)	Capillary network (+) or metameric commissures (O)	Binucleate flame cells with skeletal bars (+)	"Australian" nephridial ducts (+)	Frontal organ	Accessory lateral nerve (+)	No. of proboscis nerves	No. of stylet sacs
<i>G. nightingaleensis</i>	S (A)	L	O	O	+	+	2	O	O	O		O	19	2
<i>G. chalicophora</i>	?	T	O	O	+	+	2	O	O	O		O	12	2
<i>Acteonemertes bathamae</i>	S	L	O	O	+	+	2	+	O	O		O	15	2
<i>G. novaezealandiae</i>	S	T	O	O	+	+	2	+	O	+		O	13 to 17	4
<i>G. pantini</i>	S	T	O	O	+	+	2	+	O	+		O	13 to 17	4
Australian group	S	T	O	O	+	+	2	+	O	+		+	11 to 19	2 to 5
Pelaensis group	I	T	O	O	+	+	1	+	+	+		+	16 to 21	2 to 4
<i>G. agricola</i>	A	L	Δ	O	+	+	1	+	+	+	O	+	13 to 15	2
<i>Prosorhochmus clapedii</i>	A	L	V	O	O	O	1		+	O	O	O	10	2
<i>Prostoma graecense</i>	—	FW	O	O	O	O	1		+	O	O	O	10	2

coelenterates and of protozoa like *Epistylis* as an example of the relative ease of independent evolution of complex structures at the cellular level. But this would still leave us with the duty of relating *G. nightingaleensis* and *G. chalicophora* to the Indo-pacific species. If we start from the resemblance between the somewhat generalized *G. nightingaleensis* and the Australian species, we must account for their relation to the *pelaensis* group either by assuming that *G. nightingaleensis* has secondarily lost the accessory lateral nerve or that the *pelaensis* group which already possesses this structure has secondarily acquired its single rhynchocoelic vascular plug from the double condition seen in *G. nightingaleensis* and the Australian species. Any alternative starting point involves us equally in a number of additional assumptions. Each additional assumption weakens the force of an inductive argument for relationship.

It is, of course, quite clear that several of the characters we have discussed must in fact have been evolved independently. The difficulty in this elegant puzzle is to assess which characters can be assigned the lowest probability of independent evolution. That assessment can only be made when we have far more knowledge of those generalized littoral Tetrastemmatidae and Prosorhochmididae to which the Geonemertines are evidently related. For it is on the range and character of variation in these that our assessment of relationship must rest. The consideration of the relationship of the Geonemertine species brings out very clearly the tentative character of any "natural" classification. The arguments in favour of such classifications are in fact subjective estimates of probability and their weight must necessarily vary continually with the extent of contemporary knowledge.

But notwithstanding the uncertainty attaching to the relationship of the Geonemertine species it is certain that some characters here defined must have been independently evolved by different members. This is the more remarkable in view of the rigidity of plan of metanemertine organization; a rigidity which is so great that it would be difficult for anyone, other than a specialist, when presented with a preserved specimen of a Geonemertine to detect any fundamental departure in organization from its marine relatives—or indeed to infer that it was not a marine, but actually a terrestrial organism.

With these qualifications we may provisionally classify the species of the genus dealt with herein as follows:

Genus Geonemertes

I. Fully terrestrial

With accessory lateral nerve

With ventral cephalic furrows

With dorsal blood-vessel entering rhynchocoelic sheath

1.1. With uninucleate flame cells without skeletal bars

Without multiplication of eyes

Without rhynchocoelic plug

Without frontal organ

With few nephridial openings (about 10) (European greenhouses) *G. chalicophora*. v. Graff, 1879.

- 1.2. With rhynchocoelic plug
 - With thousands of nephridial openings.
 - 1.2.1. Without or with slight multiplication of eyes
 - With frontal organ
 - With binucleate flame cells with skeletal bars
 - With "nephridial glands" round the cephalic blood vessel
 - With single rhynchocoelic vascular plug.
 - 1.2.1.1. Red, with dark brown dorsal stripe. New Guinea. *G. pelaensis*. Semper, 1863.
 - 1.2.1.2. Seychelles. *G. arboricola*. Punnett, 1907.
 - 1.2.1.3. Dark green with single median white line. Rodriguez. *G. rodericana*. Gulliver, 1879.
 - 1.2.2. Without frontal organ
 - With uninucleate protonephridia without bars
 - With two rhynchocoelic vascular plugs
 - With multiple eyes
 - With posterior extension of glands of the cerebral organ
 - With complex nephridial ducts and radial striation
 - With vascular subdermal network.
 - 1.2.2.1. With posterior extension of glands of cerebral organ on either side of oesophagus ("oesophageal organ" of Dendy).
 - 1.2.2.1.1. With cephalic gland poorly developed and absent over brain. New South Wales. *G. hillii*. Hett, 1924.
 - 1.2.2.1.2. With well-developed cephalic gland. South-eastern Australia, Tasmania. *G. australiensis*. Dendy, 1889.
 - 1.2.2.2. With posterior extension of glands of cerebral organ lateral to brain
 - With relatively small accessory lateral nerve
 - South-west Australia. *G. dendyi*. Dakin, 1915.
- 2. Littoral
 - Without accessory lateral nerve
 - 2.1. With uninucleate protonephridia without bars
 - Without ventral cephalic furrow
 - With dorsal blood-vessel entering rhynchocoelic sheath
 - Without frontal organ
 - With two rhynchocoelic vascular plugs. Nightingale Island. *G. nightingaleensis*. Brinkman, 1947.
 - 2.2. With antero-lateral cephalic furrows
 - Without dorsal blood vessel in rhynchocoelic sheath
 - With binucleate flame cells with skeletal bars
 - With frontal organ
 - Viviparous. Bermuda. *G. agricola*. Willemoes-Suhm, 1874.

It is a pleasure to express my thanks to the many persons I have mentioned through whose kindness I had access to material from many species, and I must particularly thank Dr. Brian Boden, Dr. August Brinkmann, Dr. Wesley Coe, Miss

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APPENDIX

By JANET MOORE

Reason for deferred publication

The above paper dates from 1952. The reason for delay in publication is clear from Dr. Pantin's correspondence: "The draft is not final because after my visit to New Zealand, when I'd found *Geonemertes novaezealandiae* and *Acteonemertes bathamae*, I came to the conclusion that my divisions were on the right lines but there was still more to say, particularly about my new shore species and a redescription of *novaezealandiae* itself" (Letter to F. Crandall (University of California), May 1959). And later, "... not yet published. That is largely because I've got a very great deal more information about the New Zealand species and other species from elsewhere in the world" (Letter to Professor A. Stock, (Armidale, New South Wales), December 1962).

In 1961, however, Dr. Pantin published his Presidential Address to the Linnean Society "*Geonemertes* : A Study in Island Life" (Pantin, 1961a) and also "*Acteonemertes bathamae*, Gen. et. Sp. Nov. An Upper Littoral Nemertine from Portobello, New Zealand" (Pantin, 1961b). The first of these papers gives a preliminary report on some of the findings described in the present paper. Letters from Dr. Pantin establish that this was not intended to be a substitute for the present paper. It was written before further findings were made during Dr. Pantin's 1961 visit to New Zealand.

THE NEW ZEALAND GROUP

Referring to the present paper, Dr. Pantin wrote to F. Crandall in August 1959 : "It was written before I had studied the *Geonemertes pantini* sections and the *G. novaezealandiae* material. It was also before I had looked at my new undescribed shore nemertine, which seems closely related to the New Zealand and Australian species.

. . . My ideas have gone a good deal further since I wrote it because it was written before I went to New Zealand." (This refers to the 1954 visit : the 1961 visit produced yet more data.) Accordingly, in the present form of the paper the earlier brief account of *G. novaezealandiae* (based on restaining of slides in the collection of the late Professor Dendy) has been deleted. The following expanded version includes the second species found in New Zealand, *Geonemertes pantini* Southgate (Southgate, 1954). The account is derived from Dr. Pantin's notes on his own specimens and interpreted by study of the slides prepared from them for him by Mr. D. Buck of the Zoology Department, Cambridge.

A. *G. novaezealandiae*

1. The colour pattern consists of four dark brown dorsal bands on a cream background. The two median bands are wider and more pronounced than the two more lateral stripes (see Frontispiece).
2. There are four eyes, two large and two small.

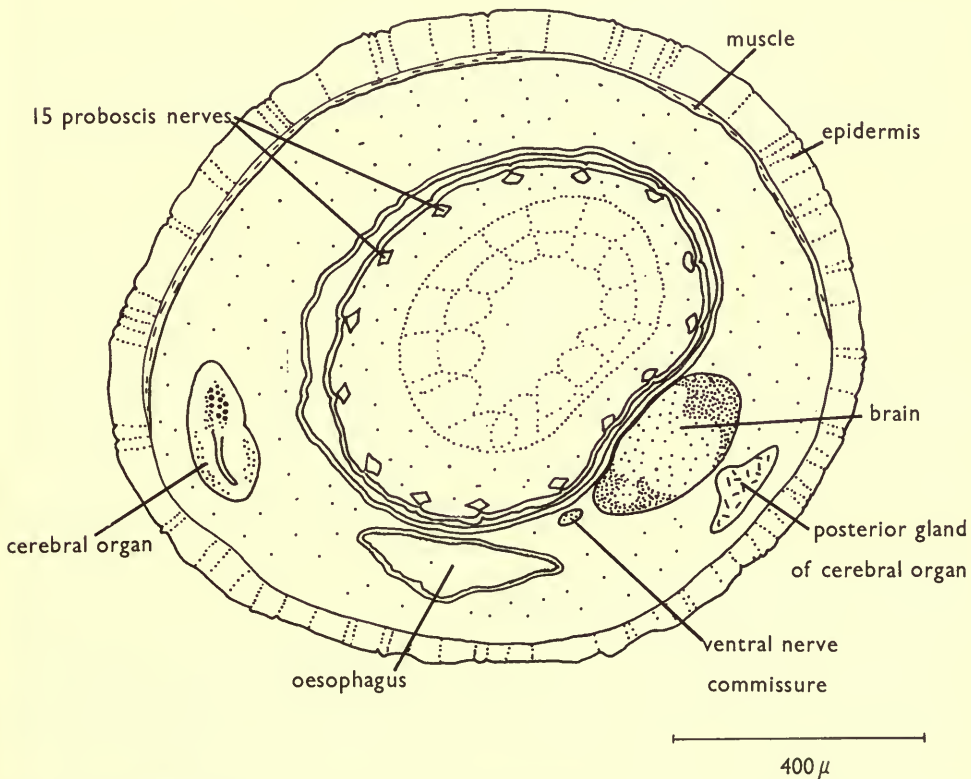


FIG. 25. Oblique transverse section *G. novaezealandiae* to show cerebral organ (cephalic gland not shown).

3. As in the Australian group, it lacks a frontal organ, though it possesses a cephalic gland. There are improvised channels for escape of the secretion.
4. The cerebral organs and their ducts are ventral and open ventrally (see Fig. 25). [There is a posterior glandular extension of the cerebral organ as in the Australian group, but it is shorter, extending backward only to anterior brain level. The extension is not as dorsal and lateral in position as in *G. dendyi* (Fig. 11). J.M.]

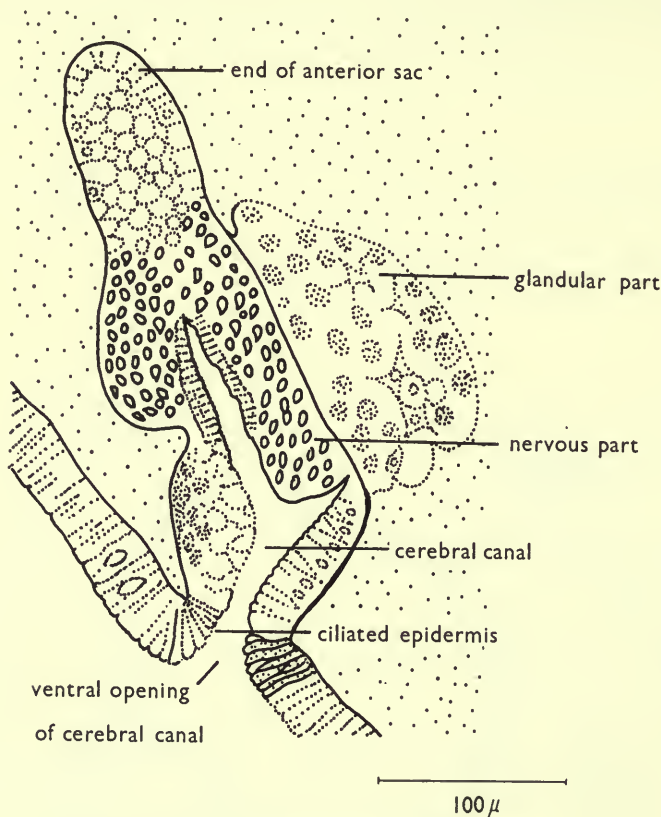


FIG. 26. Cerebral organ of *G. pantini*.

5. There are four stylet sacs.
6. There are 13-17 proboscis nerves.
7. There are two rhynchocoelic plugs from the dorsal vessel and there is a network of capillary blood vessels as in the Australian Group (cf. Figs. 14 and 7).
8. The protonephridia are uninucleate and without bars. The remainder of the nephridial system also is exactly similar to that in the Australian group, the glandular canals having thick walls with radial striations (Fig. 27).
9. Unlike both the Australian group and the *pelaensis* group, *G. novaezealandiae* has no accessory lateral nerve (Fig. 28).

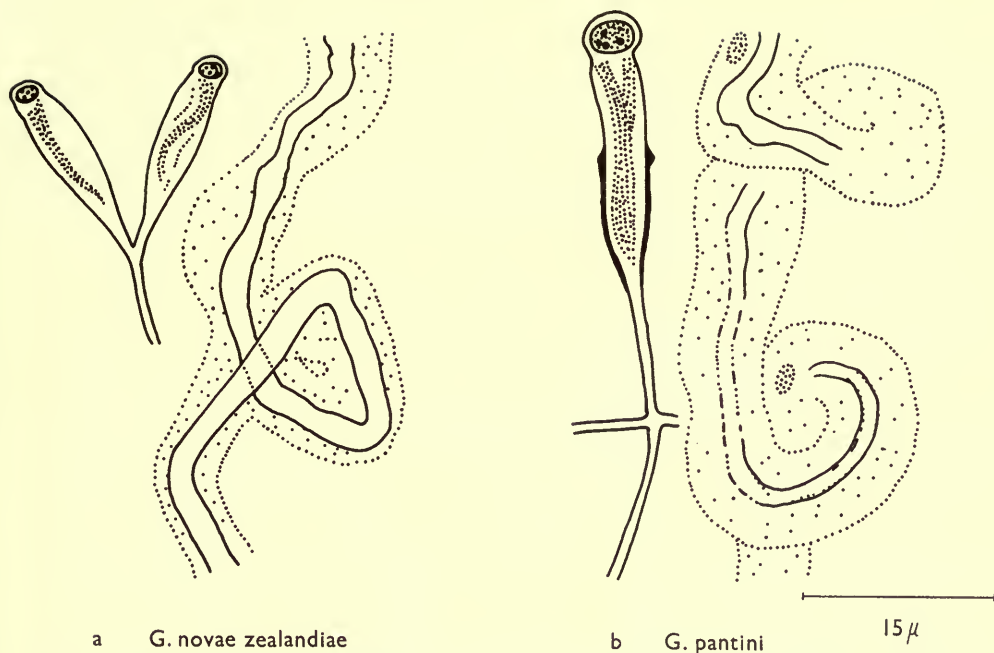


FIG. 27. Flame cells (on left) and nephridial ducts (on right) of *G. novaezealandiae* and *G. pantini*.

B. *G. pantini*

The above description of *G. novaezealandiae* applies exactly to *G. pantini* except that :

1. *G. pantini* has two warm brown stripes (see Frontispiece) of a different brown pigment, probably a melanin. "The pigment of *G. novaezealandiae* is either a porphyrin or near that chemically, while *G. pantini* has a different pigment—more insoluble. (This could be little more than a varietal difference perhaps—though it may prove to be more)." (Dr. Pantin to Mr. Southgate (Dunedin), 19th November, 1961.)
2. The accessory lateral nerve is present in *G. pantini* (see Fig. 28). "In all the specimens I have cut of either [*G. novaezealandiae* or *G. pantini*] the results are that so far as I can see they agree with each other in all their special characters which are shared with the Australian species, but like *Acteonemertes*, *novaezealandiae* has no accessory lateral nerve while *pantini* undoubtedly has one, just as in your type. This is quite extraordinary and has all sorts of implications" (Dr. Pantin to Mr. Southgate, 22nd November, 1961).

Southgate (1954) reports no accessory lateral nerve in *G. pantini*. This is because originally he followed Darbishire in considering the accessory lateral nerve to be a separate and distinct structure, instead of a separate tract of

nerve fibres within the main bundle. He later entirely agreed with Dr. Pantin's account.

3. "Another feature which I noticed in your type *pantini* was that the longitudinal muscle is organized into well-defined bundles, and I have not yet seen this to be the case in *novaezealandiae*. That might simply be due to the fact that your type specimen of *pantini* was a very fine large animal and the musculature may get more organized as an animal grows bigger" (Dr. Pantin to Mr. Southgate, 2nd August, 1960).

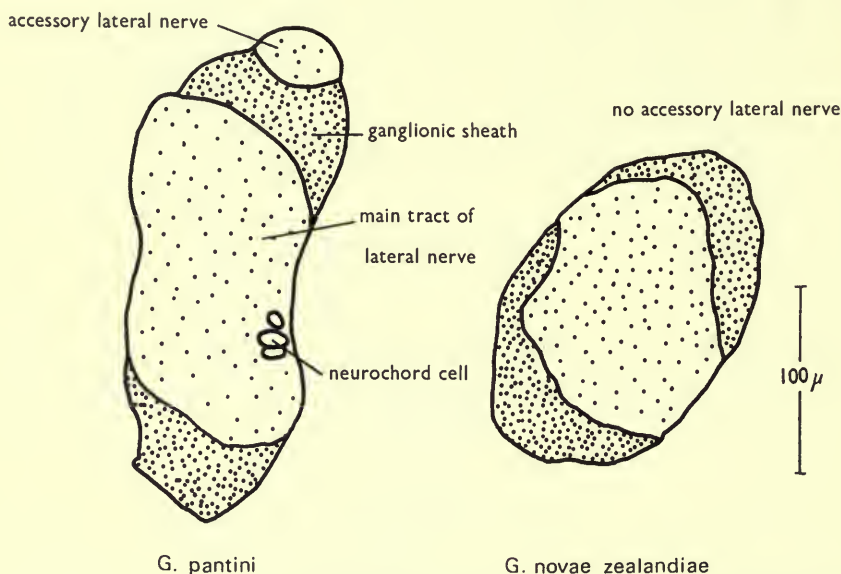


FIG. 28. Lateral nerves of *G. pantini* and *G. novaezealandiae* at the level of the first appearance of the anterior gut diverticulum (both figures show the nerve on the left of the section, with dorsal surface uppermost).

[Bearing out this last suggestion, there are sections of a very small specimen . . . "which because of its colour pattern I called *G. pantini* when I collected it". This has a small accessory lateral nerve, but does not have its longitudinal muscle in well-defined bundles. J.M.]

That the accessory lateral nerve was absent in *G. novaezealandiae* and present in *G. pantini* removed all doubt that these were two distinct species. On the contrary, "This is quite astonishing for a specific difference—it is more like a familial character" (Dr. Pantin to Mr. Southgate, 19th November, 1961).

" . . . it might suggest that the accessory lateral nerve was only evolved during the radiation of the *novaezealandiae* species. The alternative that *G. pantini* and *G. novaezealandiae* are very distantly related must, I think, be ruled out because of the very numerous other similarities of vascular system, nephridia and the rest which they possess" (Dr. Pantin to Mr. Southgate, 2nd August, 1960).

[In one specimen of *G. pantini*, the accessory lateral nerve becomes separated from the main lateral nerve and follows a separate course for some 200 μ , and then rejoins the main tract. This happens twice on the same side. During the separation, the lateral nerve cord looks just like that of *G. novaezealandiae*. J.M.]

The whole question of the significance of this character is brought in question by these two New Zealand species (see also the discussion in the main body of the paper).

"There is I think much more difference between these two species than I had first supposed, or this character is much more variable than people have generally believed and taken for granted. The answer of course will not come until I have been able to cut many specimens" (Dr. Pantin to Dr. V. V. Hickman (Tasmania), 27th October, 1961). Dr. Pantin's latest comment on the situation is: "In general the striping in the New Zealand species is certainly much more pronounced than in the Australian ones. Within the colour pattern of *G. novaezealandiae* there is certainly variation, though the underlying features of the pattern always seem to remain. However, quite apart from the variability within the pattern, there are, I am sure, real specific and subspecific differences (e.g. the presence of an accessory lateral nerve in *pantini* and its absence in *novaezealandiae*). Therefore I have paid particular attention to getting material from type localities" (Dr. Pantin to Dr. V. V. Hickman, 22nd January, 1963).

Localities where *G. novaezealandiae* and *G. pantini* were found should be recorded :

G. novaezealandiae

- (a) Toi toi, Fortrose, Nr. Invercargill, Southland, N.Z. A deserted farmhouse 3 miles south of Waimahaka on the road to Fortrose. This is a type locality (Dendy, 1895). Dr. Pantin found specimens there in 1954, but in 1961 the place was found to be unfenced and ruined by sheep.
- (b) Tokanui, Nr. Invercargill, Southland, N.Z. A wood $1\frac{1}{2}$ miles south east of Tokanui station ; a small patch of bush on the slopes of a hill. Specimens were in crevices and hollows in rotten trunks of tree ferns. (Dr. Pantin, Dr. Henry Pantin, Dr. E. J. Batham and Mr. Southgate, August 1961).
- (c) Mount Somers, near Ashburton, Canterbury, N.Z. In decomposing timber near the edge of Alford Forest at the foot of Mount Somers. Type locality (Dendy, 1895). Dr. P. M. Johns and Dr. Pantin, August 1961.
- (d) Signal Hill, Dunedin, N.Z. Dr. Pantin and Dr. E. J. Batham, 1961, but "I am not sure that the few "*G.n.z.*" specimens from Signal Hill really are *G.n.z.* and not just a colour variety of *G. pantini*" (Dr. Pantin to Dr. Batham (Portobello Marine Station), 19th November, 1961).

G. pantini

- (a) Signal Hill, Dunedin, N.Z. Type locality, (Southgate, 1954). Subsequently also found by Dr. Pantin and Dr. Batham.
- (b) Leith Valley, near Dunedin (Dr. Pantin, 1954).
- (c) Taupo, North Island, N.Z. (Dr. P. M. Johns, 1961).

C. The Menzies Bay Geonemertine

In 1961 Mrs. Allison from Christchurch (University of Canterbury) took Dr. Pantin to Menzies Bay (Banks Peninsula, South Island) where she had found a small land nemertine, and Dr. Pantin found three more specimens: "It looks very different from any of the others—possibly because they were small and perhaps immature—but I suspect a different species" (Dr. Pantin to Mr. Southgate, 15th August, 1961). One specimen was only 10 mm. long, with the dorsal surface mottled brown with a clear line over the proboscis, and only two eyes seen with a hand lens. These specimens were never sectioned, but are preserved in the Cambridge Zoology Department.

D. *Acteonemertes bathamae*

This new species was described by Dr. Pantin (1961b). It is an upper littoral marine worm which occurs on the Portobello Peninsula, South Island, and other sites in New Zealand. Its chief interest lies in its close similarity to the Australian and New Zealand species of *Geonemertes*, despite its littoral habit. It lacks an accessory lateral nerve, differing in this way from all these *Geonemertes* species other than *G. novaezealandiae*. There is, however, a small contribution from the dorsal ganglion to the main lateral nerve (Pantin, 1961b).

E. *G. spirospermia* and *G. caeca*

Two more New Zealand species of *Geonemertes* have been described, *G. spirospermia* and *G. caeca*, from the sub-antarctic Auckland and Enderby Islands (Darbishire, 1909). These descriptions are quite inadequate (see main paper). Dr. Pantin hunted in vain for Darbishire's specimens, and never examined any specimens from the outlying islands (some were kindly sent, latterly, by Dr. P. M. Johns of the University of Canterbury, Christchurch).

THE AUSTRALIAN GROUP

Dr. Pantin had intended to search for geonemertines in Australia, with particular attention to specimens from type localities.

G. hillii was sent to him by Professor A. Stock of the University of New England, Armidale, New South Wales. The orange pigment was analysed by Dr. V. H. Booth and found to be an unknown carotenoid, possibly astaxanthin. Professor Stock defines the distribution of *G. hillii* in New South Wales as follows (letter to J. M., 1st February, 1968): "We found *G. hillii* in a locality (Point Lookout)"—about 50 miles due east of Armidale—"at an altitude of about 5,000 ft. in a relatively dry situation. Since then we have found it near a place called Dorriggo (Dorriggo National Park) at an altitude of 2,400 ft. and at the edge of a rain forest and lately at the foot of Dorriggo Mountain, at 500 ft. in subtropical rain forest on the upper reaches of the Bellinger river (Bellinger river, North arm). This extends the range to the east to the edge of the coastal plain and fits in with Fletcher's (1891) find in a similar situation on the Richmond river.

"The crest of the mountain chain along the eastern coast of New South Wales seems, as far as we know at present, to be the limit to the west of the distribution of *G. hillii*."

G. australiensis has not been found in recent years at Dendy's original site in New South Wales, but has been obtained from Victoria. Specimens from Tasmania were sent to Dr. Pantin by Dr. V. V. Hickman, and these do not differ specifically from the Victorian specimens (Hickman, 1963).

Dr. Hickman has examined a large number of specimens (187 adults and 374 young) and has found a much greater range of variation than was previously recorded for the species :

Size : Males 12-60 mm., females 12-84 mm., in length (Dendy recorded "up to 40 mm.").

No. of proboscis nerves : 11-21, most often 14 (Dendy, 16-19).

No. of reserve stylet sacs : 2-11 (Dendy, 2-5).

No. of eyes : up to 170 (Dendy, 30-40, and *G. hillii* with 80 eyes was distinguished as having more than *G. australiensis* (Hett, 1924).

The colour varied from pale cream to dark reddish brown, and there was in particular variation in the degree of striping, previously considered to be an important distinguishing characteristic (Stammer, 1934). The colour may be uniform (striped and non-striped specimens may occur in the same habitat) or there may be irregular brown blotches on a cream to pale brown background. Most commonly there is a single median dorsal stripe, with or without a lateral stripe on each side, or the median stripe may be double, giving four longitudinal stripes (Hickman, 1963).

MADEIRA—THE AZORES. *G. chalicophora*?

"I have just come back from Sweden with a collection of worms from the Azores and from Madeira which Professor Dahl believes may be identical with *G. chalicophora*, the one remaining species of uncertain origin" (Dr. Pantin to Mr. Southgate, 19th December, 1961).

Professor Dahl has very kindly suggested that these slides should remain in Dr. Pantin's collection. He writes : "I was very much in doubt whether they should be regarded as *G. chalicophora* or whether they should be regarded as a new species, although I was more in favour of the first alternative. We spent most of a day over the slides and over material which Professor Pantin had brought without being able to make up our minds. However, I do think that we both tended rather to lump them with *G. chalicophora*" (Professor Dahl (University of Lund) to J.M., 20th December, 1967).

The exact localities are also recorded for all Professor Dahl's *Geonemertes* in Madeira and the Azores. No land nemertines have since been received from these islands.

THE MAURITIUS SPECIES

Land nemertines were sent to Dr. Pantin in 1962 by the late Dr. Vinson, Director

of the Mauritius Institute. These worms were found under a large stone in the dry zone of the coastal belt, "Roches Noires", and in very damp situations of the uplands.

"The structure is most interesting. It is quite clear that your worms belong to the same group which extends through from the Seychelles across the Indian Ocean to Samoa. They have all the proper features which put them in this group" (i.e. the *Pelaensis* group)—(Dr. Pantin to Dr. Vinson, 14th June, 1962).

"It would take me a little time to get round to sectioning the worms and describing them, but when I do, I should like to call this species *GEONEMERTES VINSONI*—if you would let me do so" (Dr. Pantin to Dr. Vinson, 27th August, 1963).

MISCELLANY

(a) *Recommended method of fixation*

Dr. Pantin found the best fixatives to be Susa or 80% ethyl alcohol. These methods, followed by a polychrome stain such as Mallory's triple stain or Masson's haematoxylin-Ponceau-light green, were best for bringing out details of the excretory and vascular systems. Fixatives containing acetic acid, and Bouin, should be avoided.

Two alternative prescriptions which he gave in recent years (kindly supplied by Dr. S. A. Corbet) were :

- (i) 7% ethyl alcohol until movement almost stops
- 80% ethyl alcohol to kill and fix
- 80% ethyl alcohol+5% glycerine to preserve the worms
- (ii) 7% ethyl alcohol to anaesthetize the worms
- Susa fixation
- 90% alcohol+iodine
- 90% alcohol (store in methyl benzoate).

(b) *Negative Records* : places searched for *Geonemertes* without success :

- Brazil (Dr. Pantin)
- Hawaii (Dr. Pantin, 1961)
- Canary Islands (Tenerife and Gomera) (Dr. S. A. Corbet, 1964)
- St. Helena (Mr. A. Loveridge, 1966).

(c) *Incompletely documented species*

In addition to *G. spirospermia* and *G. caeca* from New Zealand, there is another inadequately described species, *G. graffi* (Bürger, 1896) also referred to as *G. nicholitzii*, or *G. stammarai*. This species occurs in New Guinea. There are no certain differences from *G. pelaensis*.

There is also a fragment of a geonemertine in the Cambridge Zoology Museum marked "Peradeniya". (It is included as such on the world map in Pantin (1961a) with no explanation.) This specimen was collected by Dr. Punnett in Ceylon in 1909, but it could never be further traced. Dr. Pantin records "... unquestionably closely related to *G. pelaensis*. It has six eyes, a single vascular rhynchocoelic plug, and above all the typical barred, binucleate protonephridia" (Dr. Pantin to Mr. Prudhoe, 28th January, 1952).

THE "GENUS" GEONEMERTES

There is no recent record of Dr. Pantin's views about "*Geonemertes*" as a whole. The possibility of convergent evolution is discussed in Pantin (1961a).

In August 1952, Dr. Pantin wrote to Mr. Southgate: "I think probably *G. agricola* is a modified *Prosorhochmus*—and that many of the rest of the *Geonemertes* spp. are related rather to *Prostoma*." However, subsequently Dr. Pantin found the upper littoral nemertine *Acteonemertes bathamae* which is closely related to both the Australian and the New Zealand groups of species, yet is placed in the family *Prosorhochmidae* (Pantin, 1961b). Clearly Dr. Pantin's 1952 opinion must have been modified. He wrote in 1961 "It is difficult to resist the conclusion that the Australian group comprises terrestrial relatives of the marine Portobello nemertine whilst *G. agricola* may be a terrestrial relative of the marine genus *Prosorhochmus*" (Pantin, 1961a).

The question of the significance of the accessory lateral nerve was raised strongly by the finding of two apparently closely related New Zealand species, one possessing the nerve and the other lacking it (as discussed above).

In conclusion, Dr. Henry Pantin has kindly allowed me to quote his memory of discussions with his father in 1961: "I only remember that he considered their evolution to have been: marine nemertines—littoral nemertines (intertidal)—land nemertines. He also considered that this evolutionary sequence had occurred independently in widely separated localities, and had thus given rise to local varieties of *Geonemertes*. I think he believed that this evolution was in some way connected with the changes in climate and sea-level during the Pleistocene."

ACKNOWLEDGMENTS

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The following are among those who sent specimens to Professor Pantin or corresponded with him during the period 1954–66: Dr. F. R. Allison, Dr. E. J. Batham, Mr. F. Crandall, Professor E. Dahl, Dr. V. V. Hickman, Dr. M. W. Holdgate, Dr. P. M. Johns, Drs. D. S. and U. Smith, Mr. A. J. Southgate, Mr. B. W. Sparrow, Professor A. Stock, Dr. V. Stout and the late Dr. J. Vinson. J. M. would like to add her thanks to the above (also to Dr. C. Michel and Dr. H. M. Pantin) for much helpful correspondence and for permission to quote from letters.

Mrs. Pantin and Dr. Smith are grateful to the Trustees of the British Museum (Natural History) for publishing this work.

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